QUANTITATIVE GENETIC ANALYSIS OF GRAIN FILLING RATE AND GRAIN FILLING PERIOD IN TROPICAL MAIZE (*Zea mays* L.)

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My wife, Perla B. Josue

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ABSTRACT

Grain yield of maize in the tropics is limited by short days and high temperatures. Genetic information on grain filling rate (GFR) and grain filling period (GFP) in tropical maize germplasm is limited. The objectives of this study were to (1) determine genetic variation and genotype by month interactions (G x M) for GFR, GFP, chlorophyll concentration (SPAD) and other agronomic traits, (2) estimate general combining ability (GCA), specific combining ability (SCA) effects and the interactions of GCA and SCA with months for the aforementioned traits, (3) estimate non-allelic interactions for GFR and GFP using generation mean analysis (GMA), (4) determine genetic relationships among GFR and GFP with other agronomic traits, and (5) determine the effects of photosynthetic active radiation (PAR) and temperature on GFR, GFP and other agronomic traits.

Eight elite tropically adapted maize inbreds and their 28 diallel hybrids were planted in four different months in Waimanalo, Hawaii. Two GMA populations representing GFR and GFP were also planted in two Waimanalo months. Significant differences occurred among inbreds, hybrids, heterosis, G x M, GCA, SCA, GCA x M and SCA x M interactions for GFR, GFP and SPAD. Additive genetic effects were the most prevalent type of gene action for GFR, GFP, and SPAD as shown by higher ratios of GCA to SCA mean squares.

The GMA analyses of GFR and GFP data revealed little convincing evidence of departure from a simple model of additive and dominance variance, without compelling gene interactions. In some cases, the additive x dominance interactions were significant

for GFR and the dominance x dominance interactions significant for GFP. Estimates of the genetic effects were mostly confounded with the interaction components and the environment. Kernel weights were highly correlated with GFR indicating that it may be used as an effective selection index for GFR.

Photosynthetic active radiation accounted for most of the variation in GFR, GFP, kernel weight, plant yield and kernel numbers. Breeding approaches that take advantage of additive variances including hybrid breeding with evaluations in multiple environments may be used to alter GFR, GFP and chlorophyll concentration in tropical maize germplasm.

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LIST OF ABBREVIATIONS

ANOVA – analysis of variance

CER – carbon dioxide exchange rate

CV – Coefficient of variation

DAP – days after planting

DTA – days to mid-anthesis

DTS – days to mid-silk

ED – ear diameter

EH – ear height

EL – ear length

GCA – general combining ability

GCA x M – general combining ability by month interaction

GFP – grain filling period

GFR – grain filling rate

GMA – generation mean analysis

KDEN – kernel density

KN – kernel numbers

KR – kernel rows

KW – kernel weight

MPH – mid-parent heterosis

PAR – photosynthetic active radiation

PH – plant height

QTL – quantitative trait loci

SCA – specific combining ability

SCA x M – specific combining ability by month interaction

SPAD 30 – chlorophyll concentration at 30 days after planting

SPAD 60 – chlorophyll concentration at 60 days after planting

SPAD 90 – chlorophyll concentration at 90 days after planting

YLD – plant yield

CHAPTER 1
REVIEW OF LITERATURE

1.1 Stages of maize plant development

Researchers recognize two major developmental phases of the maize plant; the vegetative and reproductive phases (Kling and Edmeades, 1997; Ritchie and Hanway, 1992). The first phase is characterized by the emergence of the coleoptile from the ground during seed germination (V_E), development of the leaves, and emergence of the last tassel branch (V_T) which takes place around 55 days after planting (Kling and Edmeades, 1997) (Table 1.1). The second phase begins with anthesis or pollen shedding (R_0) followed by silk emergence and stages of grain filling until physiologic maturity (R_6) often indicated by formation of a black abscission layer at the base of the kernel (Table 1.1). The abscission layer functions as a physical barrier that prevents further uptake of assimilates by the kernel (Daynard, 1969; Daynard, 1972). This first phase (V_E to V_T) and second phase (R_0 to R_6) are also described as the development and completion of fruiting structures, respectively (Salvador and Pearce, 1995). The transitions between the stages of development are not discrete and may overlap. The details of the major stages of maize plant growth are presented in Table 1.1 (Kling and Edmeades, 1997).

In Waimanalo, Hawaii, the length of the vegetative phase to the onset of anthesis is seasonally dependent. This phase takes 50 to 70 days with completion of dry matter accumulation at around 100 days (Brewbaker, 2003). Days to anthesis is extended in winter by about 5 to 7 days for sweet corn hybrids because of lower temperatures. Field

corn hybrids mature in about 100 days during the summer months and take 10 days longer during the winter.

Table 1.1. Growth stages of maize.

Stage	Description
V_E	Emergence of coleoptile
V_1, V_2	Development of first and second leaf collar or plumule, respectively
V*n*	The final number of leaves is denoted by *n* which is usually 16-23. The lower 4-7 leaves then senesce at flowering
V_T	Emergence of the last tassel branch
R_0	Anthesis
R_1	Silk emergence
R_2	Blistering stage. Clear fluid fills the kernels and embryo visible
R_3	Milking stage. A white milky fluid forms on the kernels
R_4	Dough stage. Kernels become filled with white paste, embryo grows about 50% the size of the kernel.
R_5	Dent stage.
R_6	Physiologic maturity. Characterized by the formation of a black abscission layer at the base of the kernel

1.2 Stages of grain filling

Regression analysis was used by Johnson and Tanner, (1972) to describe maize grain filling events in terms of rate and duration. These events were divided into three phases: 1) lag phase, 2) linear filling phase, 3) leveling-off of dry matter accumulation. A recent system of nomenclature (Salvador and Pearce, 1995) divides the Johnson and Tanner lag phase further into the dilatory and exponential phases. The leveling-off of dry matter accumulation was termed the attenuative phase.

The grain filling phase is preceded by the flowering period in which tassel and silks emerge, pollen is shed, and syngamy and fruit set occur. Salvador and Pearce

(1995) described this sequence of events as the gestational period. The three major phases of grain development are discussed below.

1.2.1 Lag phase

The lag phase lasts from syngamy until the start of the accumulation of dry matter starch in the amyloplast. This phase is characterized by the development of endosperm cells and their components required for starch synthesis (Reddy and Daynard, 1983). The endosperm comprises about 80% of the kernel weight and is about 90% starch in field corns (Brewbaker, 2003). Johnson and Tanner (1972) calculated the length of the lag phase by using a weighted regression analysis of time and weight by reversal of the independent (weight) and dependent (time) variables. The resulting regression equation was used to calculate B which was defined as the end of the lag period (A-B) when yield was 0, where A was the silking date and B was the lag period. While using a value of 0 for yield may present errors, this was assumed to be small and insignificant since the smallest values used for calculating the regression were close to 0. Another approach was used to calculate the lag period based on thermal units (Cross, 1975). In this procedure, a heat stress equation (Cross and Zuber, 1972) was first calculated using a high and low base temperatures recorded at the experimental site. In the Cross (1975) study, a preliminary plot of the data from a set of 21 hybrids grown at Fargo ND showed that at 300 thermal units, all of the hybrids had reached the beginning of the linear filling phase. This equation was then used as the reference point to calculate the regression

equation to determine the linear filling phase. The lag period was reported as the thermal units accumulated from the day of silking to a mean kernel dry weight (10.0 mg).

Recent literature shows some refinement of the lag phase concept. This phase was subdivided by Salvador and Pearce (1995) into dilatory and exponential phases. As described, the accumulation of dry matter is slow in the dilatory phase and biosynthetic activity is high. The exponential phase follows the dilatory and linear filling phase (Lemcoff and Loomis, 1986) in which dry matter accumulation begins to accelerate on a per ear basis at a constant high rate that progresses from the base to the tip of the ear. Salvador and Pearce (1995) also indicated that full kernel development or fruit set coincides also with the exponential phase and it is in this phase that the final number of kernels predestined to become physiologically mature are determined.

1.2.2 Linear filling phase

The linear filling phase is characterized by constant rapid accumulation of dry matter and it comprises the longest and largest portion of grain development. This is also known as the relative length of the actual grain filling period. Two attributes that characterize linear filling phase are; 1) grain filling rate (GFR) and, 2) grain filling period (GFP) or duration.

1.2.2.1 Grain filling rate

Regression analysis is used to calculate GFR and is expressed as the slope of the linear regression of kernel weight (Y) and time (X) until physiological maturity. Time

may be expressed in days after pollination (Wang et al., 1999) or accumulated thermal units. Cross (1975) expressed GFR as the gain in kernel weight per 1000 thermal units for the period starting from 300 thermal units after silking until 95% of dry matter accumulation was reached. Johnson and Tanner (1972) used the same approach, without the inclusion of thermal data. Temperature may be taken into account in calculating grain filling rates when there are extreme temperature differences (e.g. between night and day) throughout the growing period.

In Hawaii, field corn inbred lines fill at a rate of 7-8 mg kernel^{-1}day^{-1} at 28°C and slow down to 4-5 mg kernel^{-1}day^{-1} due to lower temperatures during the colder months (Brewbaker, 2003). Tropical x temperate single cross hybrids grown at Waimanalo filled at a rate of 5.3 to 9.1 g day^{-1} during the summer (Fahrner, 1991).

The end of the linear phase was determined by Cross (1975) by calculating a regression equation using kernel samples taken at interval starting at 300 thermal units after silking, and predicting the thermal units needed to attain 95% of the final mature dry weight. Samples taken beyond the 95% prediction were excluded before computation of a final regression equation. Johnson and Tanner (1972) calculated the end of this filling period to 90% of the final yield.

1.2.2.2 Grain filling period

Three methods are used to determine the length of the grain filling period in maize. First, is the days to the formation of the black abscission layer at the kernel placents (Daynard and Duncan, 1969). This layer prevents translocation of assimilates to

the kernel, terminates grain filling and is an indication of physiologic maturity. The second method is determine mathematically, by dividing the final kernel weight at maturity by the grain filling rate (Johnson and Tanner, 1972). Third is at 35% grain moisture (Sala et al., 2007). The first two measures were compared by Daynard and Kannenberg (1976). The first method is referred to as the actual filling period duration (AFPD) and the second as the effective filling period duration (EFPD) (Daynard and Kannenberg, 1976). Both methods are highly correlated and account for a similar proportion of the total variation in hybrid yield. The correlation coefficient between yield and AFPD was 0.56, while yield and EFPD was 0.53. Both methods were found to be equally effective in measuring grain filling periods among genotypes.

1.2.3 Leveling off of dry matter accumulation and black layer formation

Black layer formation in maize kernels was first described in detail by Kiesselbach and Walker (1952). During early seed development, the black closing layer develops in several layers of cells between the basal endosperm of the kernel and vascular area of the pedicel. These cells eventually shrink when physiologic maturity is approached and condense into a visible black layer. Concomitantly the basal endosperm conducting cells become disorganized and tangential crushed and ceases their translocation functions. This disorganization is followed by formation of a suberized barrier around the seed that results as the black closing layer merges with the testa and pericarp (Kiesselbach and Walker, 1952). This phase is also termed the attenuative

phase and is characterized by a decrease in metabolic activity, and decrease in sugar uptake (Salvador and Pearce, 1995).

The relationship between black layer formation and grain maturity in maize was studied by Daynard and Duncan (1969) in Lexington, KY using four commercial hybrids. Days to black layer formation was found to be highly correlated with the predicted date at which maximum kernel dry weight is attained. Daynard and Duncan (1969) further examined 60 hybrids which included flint, dent, yellow and white endosperm types, sweet corn, pop corn and South American races with wide ranges of maturity. All hybrids grown in Kentucky developed a black layer at the placental region of the kernels and the authors concluded that it could be used as a simple and precise indicator of maximum kernel weight and an effective selection tool for breeders to extend grain filling periods. In this region, later stages of grain fill occur under increasingly cold temperature, even frost. Although the appearance of black layer may be an effective indicator of kernel maturity, it may be induced prematurely at lower temperatures (Daynard, 1972). Indeed it may not be evident in some environments as reported in Argentina by Maddonni et al. (1998), and is often difficult to see in Hawaii. In this study, some of the diallel hybrids did not show any black layer formation at physiologic maturity.

1.3 Factors affecting the rate and duration of grain filling

1.3.1 Temperature

The length of the filling period is greatly influenced by temperature. Grain filling rates may be expressed on either a per day or thermal basis when uniform or highly variable temperatures prevail during the growing period, respectively. Grain filling periods are prolonged by lower temperatures, and grain yields were also observed to increase at higher temperatures. In Waimanalo, Hawaii, where average monthly temperatures varies from 21.8 to 25.8°C, grain yield of maize is found to be compensated at lower temperatures by an extension of the grain filling period and increase in light interception (Jong et al., 1982). In an experiment conducted under controlled environment conditions, grain yield of a single cross hybrid, Guelph GX 122 was reported by Badu-Apraku et al. (1983) to be reduced at high temperature (35°C) because of a reduction in the duration of grain filling. Cirilo and Andrade (1996) in Balcarce, Argentina reported that the effective filling period was highly dependent on assimilate supply and temperature, increasing to about 0.3 mg day^{-1} $°C^{-1}$.

Several studies have shown that the temperature had no significant effects on the rate of grain filling in maize, wheat and in rice. Badu-Apraku et al. (1983) reported that temperature had no significant effect on grain filling rate per se during the linear phase of filling in maize hybrid under controlled environment growth cabinets. Experiments with wheat (*Triticum aestivum* L.) have shown that a temperature increase from 15-20°C, from 21 to 37 days post anthesis, did not significantly increase grain filling rate (Ford and Thorne, 1975). Further, in field grown rice, high temperatures during the grain filling

period did not affect the rate of dry matter increase (Kobata and Uemuki, 2004). In wheat, grain filling period is shortened under high temperatures of 30/25°C (day/night) that resulted in a significant reduction in grain weight but did not affect grain filling rate (Zahedi and Jenner, 2003). It is also found out that with prolonged temperatures of up to 30°C, grain weight in wheat is reduced as a result of a reduction in the grain filling period (Sofield et al., 1977). The wheat grain filling duration is reduced to about 3 days for every 1°C increase in mean temperature (Wiegand and Cuellar, 1981). At a temperature ranges of 20-30°C, the magnitude of change in grain filling rate in wheat is less affected compared to grain filling period and that the change is due more to cultivar type, environmental factors and nutrient availability (Hunt et al., 1991). The slight increase in the rate of dry matter accumulation at 20-30°C, is not enough to compensate for the decrease in kernel weight caused by the shortening of the grain filling period (Tashiro and Wardlaw, 1990; Wardlaw et al., 1990).

1.3.2 Light

Solar radiation is a major determinant of yield productivity in maize as well as other cereal crops. In Hawaii, daylight range from 10.75 to 13.25 hours and is a major limiting factor in maize grain yields (Brewbaker, 2003). Yield reductions are more pronounced in windward areas during the winter months where overcast skies further reduce incident light. Grain yield and yield components are found to follow a cyclical change with solar radiation based on 41 monthly plantings of maize hybrids at Waimanalo, Hawaii (Jong et al., 1982). In this study, yields ranged from 3.5 to 11.5

metric tons ha^{-1} and were highly correlated with incident light that ranged from 216 to 507 cal cm^{-2} day^{-1}. Muchow (1989) also reported that higher incident radiation could compensate for yield reductions caused by high temperatures during grain fill. In a study by Tollenaar (1999) in controlled growth cabinets, photoperiod and photosynthetic photon flux density (PPFD) did not affect the length of the grain filling period in maize, from silking to half-milk line or from silking to black layer formation.

1.4 Relationship of the rate and duration of grain filling to other yield components

An approach to increase yield can involve increasing grain filling rate in areas with short growing seasons (Daynard and Kannenberg, 1976; Jones et al., 1979), or extending the grain filling period to take advantage of light in areas with longer growing seasons (Carter and Poneleit, 1973; Poneleit and Egli, 1979). Breeding for the improvement of both traits has been has been an objective of many research studies in maize, wheat and in rice.

The final kernel weight is a result of kernel growth that takes place during the lag and effective filling phases. Daynard et al. (1971) reported that yield is positively correlated to the effective filling period duration. Linear regression analysis showed that 71-80% of total variation in yield differences could be explained by differences in the effective filling period duration. Similarly, Cross (1975), obtained a phenotypic correlation coefficient of 0.81 between grain filling period and yield in maize. Perenzin et al. (1980) reported a positive correlation between the duration of grain filling and kernel weight based on a study of 40 Italian open pollinated maize varieties. In this

study, correlation coefficients for the length of the filling period and kernel weight were 0.672 (year 1), 0.487 (year 2) and 0.581 (combined years), and were significant at the 1% level of probability. High heritability estimates for grain filling period indicated that selection would be effective in increasing grain filling period. Pe' et al. (1982) also reported that grain filling period was related to plant yield using factor and path coefficient analysis. Lastly in rice, Jones et al. (1979) found a significant phenotypic correlation of 0.70 between grain filling rate and grain yield

Grain yield in wheat was not found to be associated with grain filling period in fifty $F_{3:5}$ progenies from 12 spring wheat crosses (Talbert et al., 2001). In another set of 20 spring wheat lines, grain yields and kernel weights also were not associated with grain filling periods (Bruckner and Frohberg, 1987).

Hartung et al. (1989) examined the responses to selection of grain filling rates and durations after three cycles of recurrent selection in populations- two with short vs. long EFPD, and two with high vs. low GFRs. Half sib selection significantly prolonged the EFPD, while GFR in cycle 3 was found to be 13% greater than the initial population. Yield response after selection was low in the long EFPD population, and the selection led to reduced GFR, which was also due to reduced kernel number and size. Kernel weight and number were both influenced by GFR, and kernel weight by EFPD.

1.5 Photosynthesis and grain yield

Richards (2000) reported that genetic increase in the rate of photosynthesis per unit leaf area has not yet been achieved in plants despite intense selection for improved yield. Yield increases were attributed mainly to (1) extended photosynthesis per unit land area, contributed primarily by improved agronomic practices, and, (2) increased partitioning of crop biomass to harvested product, achieved mainly through plant breeding. Richards suggested that a possible contributing factor to the lack of increased photosynthetic rate is the increased use of nitrogen fertilizer. Nitrogen increases leaf area, leaf area duration and leaf nitrogen content, all of which result in an increase in photosynthesis per unit ground area. Under these favorable conditions, selection pressure for plants with increased photosynthetic rate becomes ineffective since higher rates of photosynthesis per unit ground area have already been achieved.

The genetics of photosynthesis in maize was studied by Crosbie et al. (1978) using a complete diallel among eight inbred lines derived from the Iowa Stiff Stalk synthetic (BSSS) line. These inbreds were selected to represent low and high leaf CO_2 exchange rates. Shibles (1976) initially defined CO_2 exchange rate as an estimate for photosynthesis for the BSSS population. Crosbie et al. (1978) measured leaf CO_2 exchange rates during the vegetative and grain filling stages of growth. Results showed that general combining ability (GCA) effects were 9.4 and 4.8 times larger than specific combining ability effects for CO_2 exchange rates at vegetative and grain filling stages of growth, respectively, suggesting that CO_2 exchange rates were predominantly controlled by additive gene effects.

The SPAD-502 chlorophyll meter was developed by Minolta Corporation as non-destructive, quick and relatively cheap method of measuring leaf chlorophyll concentration. Chlorophyll has two spectral absorbance peaks one in; the blue (450-480 nm) and the other in the red (650-680). The lowest absorbance occurs in the green region with no absorbance in infrared region. The meter works by emitting red and infrared LEDs (light emitting diode) that passes through the leaf and onto a receptor that converts the light into analog electrical signals. These signals are subsequently converted into digital signals by an analog-digital converter and used by a microprocessor to calculate SPAD values (Minolta, 1989). Wang et al. (1999) found a positive genetic correlation of SPAD chlorophyll concentration with single plant yield (r=0.73). Chlorophyll concentration had a small direct effect on grain yield, and large indirect effect on yield through kernel number per ear and grain-filling duration. In rice, Murchie (2002) compared grain filling rate (dry matter accumulated per panicle per day) to rate of photosynthesis per unit leaf area in five new plant type (NPT) tropical japonica varieties, and one indica variety, IR72. For the IR72 variety, a decline in the light saturated rate of photosynthesis coincided with the rapid phase of grain filling. For the NPT varieties, no relationship was found between grain filling and rate of photosynthesis.

Chlorophyll concentration has been used as an indicator to determine the nitrogen requirements in maize. Piekielek and Fox (1992) found that the use of a Minolta SPAD chlorophyll meter was accurate in distinguishing nitrogen responsive and non-responsive sites compared to the following soil nitrogen tests; (1) soil NO_3 concentration of the 20cm soil surface at planting, (2) soil NO_3 concentration of the 30cm soil surface taken before

side dressing with N fertilizer (4-5 weeks after emergence), and (3) UV absorbance at 200nm of a 0.01 M $NaHCO_3$ extract of 20m soil surface sampled during planting. Measurements were taken at the six-leaf growth stage and the SPAD reading of the fifth leaf was the best indicator of response to N fertilizer applied as side dress.

1.6 Genetics of grain filling

Several studies have revealed that the rate and duration of grain filling in maize is controlled predominantly by an additive type of gene action. A diallel analysis among 7 inbred lines for the rate and duration of grain filling in maize was studied by Cross (1975) using Method 4 (Griffing, 1956) with one set of F1 crosses in a diallel. Significant differences ($P<0.01$) for grain filling period and grain filling rate were found among the hybrids grown at Fargo, N. D. No significant differences were found in lag period among the hybrids. Computation of general (GCA) and specific (SCA) combining ability effects revealed that GCA effects were the most prevalent type of gene action for grain filling period ($P<0.01$), grain filling rate ($P<0.01$), grain yield ($P<0.01$) and the lag period ($P<0.05$).

In a related study, Ottaviano and Camussi (1981) determined GCA and SCA effects for lag period, effective filling period duration, and grain filling rate in a diallel among 10 maize inbred lines that included inbreds B73 and Mo17, both of which are known for their good combining ability. The study was conducted in three environments, two years at Milano and one year at Pavia, Italy. Inbred Mo17 had the highest GCA effect (0.637) for grain filling rate, and B14 had the highest GCA (2.583) for effective

filling period duration. Similar to the findings of Cross (1975) and Wang et al. (1999), GCA to SCA ratios were highest for grain filling rate and effective filling period duration. Greater GCA mean squares were also observed for lag phase, kernel row number, kernels number per row and yield per plant. Environment (E) x SCA interactions were not significant for majority of the traits studied except grain moisture, and yield per plant while E x GCA effects for grain filling rate and effective filling period duration were all highly significant ($P<0.01$).

In another study, Wang et al. (1999) examined GCA and SCA effects for grain filling rate expressed on a per kernel and per ear basis, and grain filling duration using 8 inbred lines crossed in a 4 x 4 mating scheme (North Carolina Design II) at Baton Rouge, Louisiana. Combining ability analyses revealed that GCA effects explained most of the variation in kernel filling rate, effective filling period duration, and black layer maturity ($P<0.01$), while SCA was most important for ear filling rate and kernel number ($P<0.01$).

While most studies indicate the prevalence of additive gene effects for grain filling rate and grain filling period, a study by Fahrner (1991) in Hawaii showed that these traits are controlled mainly by non-additive gene effects. The 6 inbred lines used were crossed in a diallel and grown at Waimanalo and Kapaa. Variation in grain filling was mainly due to SCA effects, as evidenced by a GCA to SCA ratio of 0.71. Similarly, SCA effects were more prevalent than GCA for grain filling period (GCA/SCA = 0.66).

Generation mean analysis was used in spring wheat to study gene effects for grain filling rate in four different parental crosses (Mashiringwani et al., 1994). Additive and dominance gene effects were most prevalent in the genetic control of grain filling rate in

the main and whole plant ears. Genetic control of grain filling rate in the last ears was primarily due to additive and additive x additive epistatic effects.

1.7 Concepts of general (GCA) and specific combining ability (SCA)

The ultimate factor in determining the usefulness of inbred lines in hybrid combinations is the information on their combining abilities (Hallauer and Miranda, 1988). Falconer (1989) defined general combining ability (GCA) as the mean performance of a parent line in several cross combinations that is expressed as deviation from the mean performance of all crosses, and specific combining ability (SCA) as the deviation (+ or -) of a cross from its expected value (which is the average of the general combining abilities of each parent in that cross). Falconer (1989) explained that GCA is a main effect and SCA is an interaction. The presence of additive gene effects is described primarily by GCA, while the presence of dominance and epistatic gene action is described by SCA.

A diallel is defined as a set of all possible crosses among a set of inbred lines (Hayman, 1954). This mating design is used to measure GCA and SCA for certain traits such as yield. Diallel analysis could be performed based on fixed or random effects model (Griffing, 1956; Hayman, 1954). In place of inbred lines, populations or varieties could also be used (Gardner and Eberhart, 1966). The two-factor diallel mating design is the most extensively used in maize breeding. Griffing (1956) described four methods of diallel analysis which are as follows; Method 1- includes parents, F1s and the reciprocals (where, p^2= number of genotypes (g), and p= number of parents), Method 2 - parents and

the F1s without the reciprocals (g = p(p+1)/2), Method 3 - F1's and the reciprocal crosses only (g= p(p-1)), and Method 4 – one set of F1 crosses only (g = p(p-1)/2).

The analysis of variance for diallel analysis follows a randomized complete block that emphasizes the hybrid (F1) main effect that is partitioned into GCA and SCA.
The basic model used is as follows (Brewbaker, 2004):

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + e$$

Where Y_{ij} is the hybrid mean, μ hybrid mean effect, g_i and g_j are GCA effects of parents i and j, s_{ij} is the hybrid SCA effect, and e the experimental error.

1.8 Generation mean analysis (GMA)

Generation mean analysis provides information on additive, dominance and epistatic modes of gene action. The analysis also divides epistasis or the non-allelic interactions into; additive x additive, additive x dominance and dominance x dominance interactions. Mather and Jinks (1982) used the notation *d* to reflect additivity, ***h*** for dominance, and *i*, *j*, *l* to reflect additive x additive, additive x dominance, and dominance x dominance interactions, respectively.

Observed means and variances from various generations are utilized by generation mean analysis. These generations are derived from a cross between 2 homozygous lines, each of which should be contrasting for the trait of interest (e.g. high x low grain filling rate). The following generations are to be included in the GMA: parents

P_1 P_2, F_1, backcrosses B_1, B_2, and F_2. The concepts of the GMA discussed below were reviewed from Mather and Jinks (1982), and Singh and Chaudhary (1985).

1.8.1 Individual scaling test

The variances of the generation means are taken into account when testing for the conformity to the additive-dominance model. The following are the tests based on Mather's (1949), formula

$$A = 2\overline{B}_1 - \overline{P}_1 - \overline{F}_1 \qquad V_A = 4V\overline{B}_1 + V\overline{P}_1 + V\overline{F}_1$$

$$B = 2\overline{B}_2 - \overline{P}_2 - \overline{F}_1 \qquad V_B = 4\,V\overline{B}_2 + V\overline{P}_2 + V\overline{F}_1$$

$$C = 4\overline{F}_2 - 2\overline{F}_1 - \overline{P}_1 - \overline{P}_2 \qquad V_C = 16V\overline{F}_2 + 4V\overline{F}_2 + V\overline{P}_1 + V\overline{P}_2$$

If the additive dominance model is adequate, the quantities A, B and C will be equal to 0 within the limits of sampling error. The standard error of A is obtained by $\sqrt{V_A}$ and test of significance using the t-test. The additive-dominance model would be perfectly adequate if the values of A, B and C were not significant (deviations from 0 are not significant). Singh and Chaudhary (1985) explained that if any of the scales were significant this would then indicate presence of non-allelic interaction and the additive-dominance model be deemed inadequate.

1.8.2 Joint scaling test

This type of test takes into account all parameters unlike the individual scaling test which takes them one at a time. This test was developed by Cavalli (1952) which

consists of estimating the parameters *m*, [*d*] and [*h*] (often called a three parameter model). Briefly, as outlined in Mather and Jinks (1982), the parameters are estimated by weighted least squares, that is the reciprocal of the standard errors of each generation mean. This test also incorporates a test for goodness of fit (requires at least 4 families) for the model. The six equations (from each generation) are combined to give three equations that yield the weighted least squares estimates of the three parameters. Another approach would be through matrix algebraic analysis as described by Mather and Jinks (1982) and Rowe and Alexander (1980). Singh and Chaudhary (1985) explained that when an *n* parameter model is fitted, and if *p* out of *n* estimates are non-significant, the model should be refitted with *n-p* parameters until all parameters are significant.

1.8.3 Detection of non-allelic interaction

Failure to observe relationships between generation means expected from the additive dominance model by the individual or joint scaling tests indicate the presence of non-allelic gene interactions. Mather and Jinks (1982) defined expectations for the scaling tests in the presence of non-allelic interactions. In addition to A, B and C above, D provides test for the *i* type of interaction, where:

$$D = 4\overline{F}_3 - 2\overline{F}_2 - \overline{P}_1 - \overline{P}_2$$

The test C largely depends on the *l* type of interaction, while the combination of C and D gives an assessment on the importance of *i* and *l* interactions. The backcross tests A and

B will be affected by the *j* type of interaction. The presence and magnitude of non-allelic interactions can be detected provided that sufficient generation means are available. A model was outlined by Jinks and Jones (1958) that included the parameters *m*, [*d*], [*h*], [*i*], [*j*], and [*l*], and often called the six-parameter model, where:

$$m = \tfrac{1}{2}\overline{P}_1 + \tfrac{1}{2}\overline{P}_2 + 4\overline{F}_2 - 2\overline{B}_1 - 2\overline{B}_2$$

$$[d] = \tfrac{1}{2}\overline{P}_1 - \tfrac{1}{2}\overline{P}_2$$

$$[h] = 6\overline{B}_1 + 6\overline{B}_2 - 8\overline{F}_2 - \overline{F}_1 - 1\tfrac{1}{2}\overline{P}_1 - 1\tfrac{1}{2}\overline{P}_2$$

$$[i] = 2\overline{B}_1 - \overline{P}_1 - 2\overline{B}_2 + \overline{P}_2$$

$$[l] = \overline{P}_1 + \overline{P}_2 + 2\overline{F}_1 + 4\overline{F}_2 - 4\overline{B}_1 - 4\overline{B}_2$$

In the usual way, the standard errors are obtained as

$$V_{[d]} = \tfrac{1}{4}V\overline{P}_1 + \tfrac{1}{4}V\overline{P}_2$$

$$S_{[d]} = \sqrt{V_{[d]}}$$

and the significance of [*d*] can be tested by $t = [d] / S_{[d]}$.

CHAPTER 2
DIALLEL ANALYSIS OF GRAIN FILLING RATE AND GRAIN FILLING PERIOD IN MAIZE

2.1 Introduction

This study was conducted to determine general (GCA) and specific (SCA) combining ability effects for grain filling rate (GFR) and grain filling period (GFP) in maize. Eight elite maize inbred lines representing diverse heterotic groups with tropical and temperate backgrounds were crossed in a diallel. Hybrids and inbreds were evaluated in four Waimanalo planting dates with two replications in a randomized complete block. The diallel trials were planted on July 2004 (7/04) and August 2004 (8/04), March (3/05) and May (5/05). The relationship of GFR and GFP to other agronomic traits and climatic factors such as temperature and photosynthetic active radiation (PAR) during the growing period were determined using correlation analysis.

Individual mean performances of the inbreds and their hybrids were calculated for GFR and GFP within and across Waimanalo planting dates. Inbred means and their corresponding hybrid array means for GFR and GFP were also compared and their variance analyzed. Grain filling data for the experiment conducted in 7/04 was excluded in the analysis because of inadequate sampling points during the growing period to calculate a regression to determine GFR and GFP (only ears at 14 and 35 days were harvested).

2.2 Materials and Methods

2.2.1 Waimanalo climate conditions

Mean monthly temperature recordings during the growing period from 2003 to 2005 at Waimanalo, Hawaii ranged from 21.8 to 26.9°C, the lowest of which occurred in January and highest in August and September (Figure 2.1). Throughout 2003 to 2005, mean minimum temperature occurred in January (17.9°C) while mean maximum temperature occurred in September (30.3°C) (Figure 2.2). The trends in temperature followed the temperature records obtained from 1980 to 2000 at Waimanalo (Figure 2.1).

Photosynthetic active radiation (PAR) (mol $m^{-2}day^{-1}$) was measured from January to December 2005 and 2006. Measurements of PAR were made using a quantum light sensor (Spectrum Technologies, Plainfield IL). Readings were not available during the 2004 plantings. Figure 2.3 shows the mean monthly PAR recorded at Waimanalo from January to December 2005 and 2006. The lowest PAR reading occurred in January (16.7 mol m^{-2} day^{-1}) while the highest readings were observed in June (43.8 mol $m^{-2}day^{-1}$), July (42.4 mol $m^{-2}day^{-1}$), and August (41.9 mol $m^{-2}day^{-1}$). Levels of PAR started to decline beginning September (42.7 mol $m^{-2}day^{-1}$) as the cool month approached.

The mean rainfall in 2004 and 2005 varied considerably from the 20 year average from 1980 to 2000 (Figure 2.4). Average rainfall was highest in 2004 in the months of January (16.7 inches), and February (14.5 inches). The mean amount of rainfall in January (2003-2005) pattern was almost 2 times greater than the mean amount of rainfall recorded from 1980 to 2000 (6.9 inches).

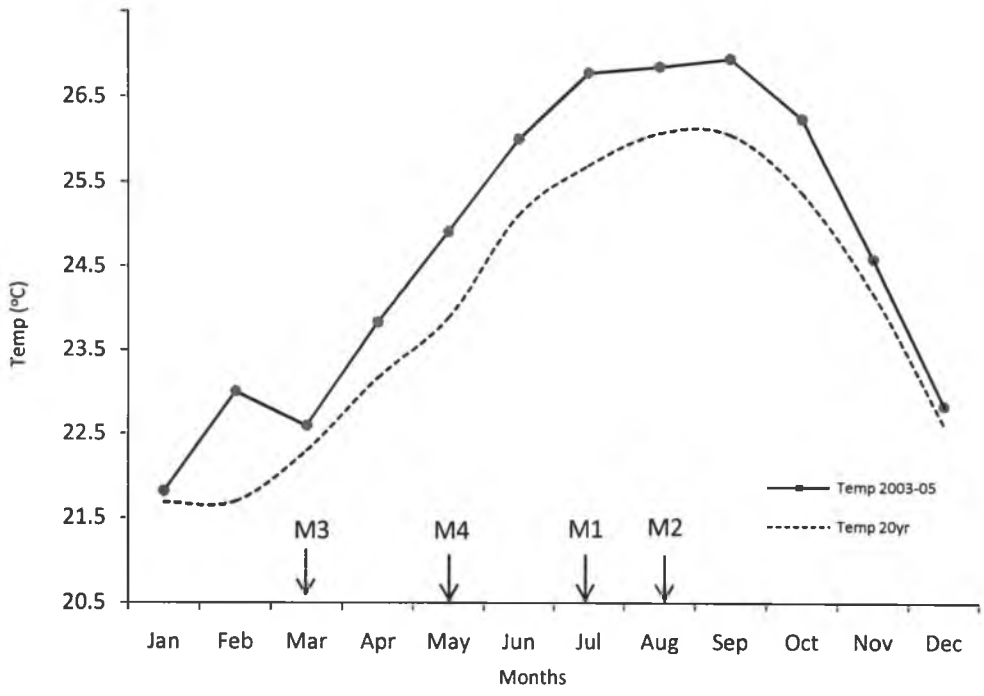

Figure 2.1. Average temperature from 2003-2005 and 20 year period (1980-2000) at Waimanao Hawaii, where M1, M2, M3, M4 were the months at which the diallels were planted.

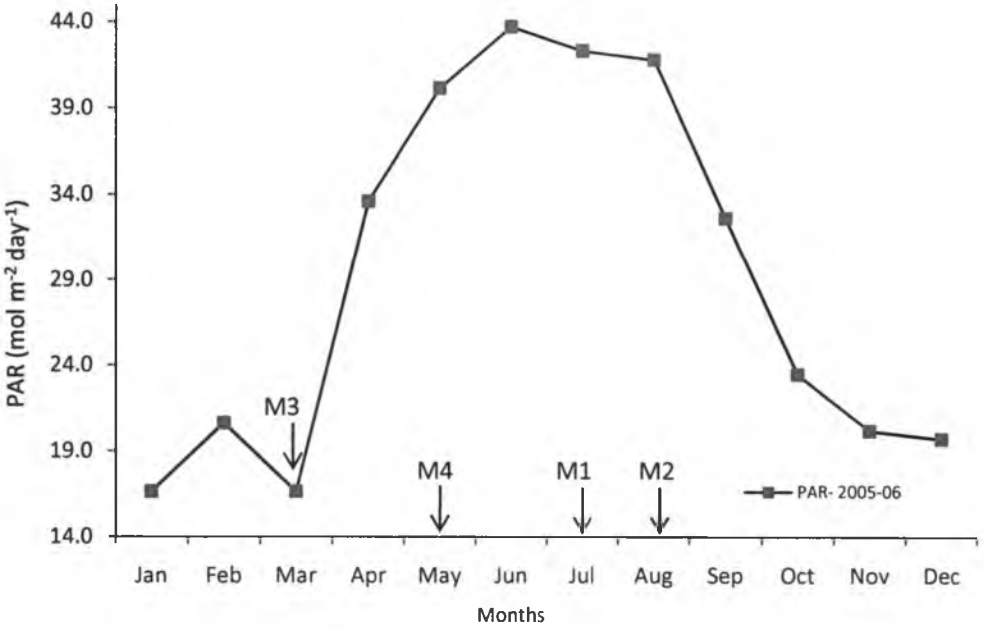

Figure 2.2. Average monthly photosynthetic active radiation at Waimanalo, Hawaii from 2005-2006, where M1, M2, M3, M4 were the months at which the diallels were planted.

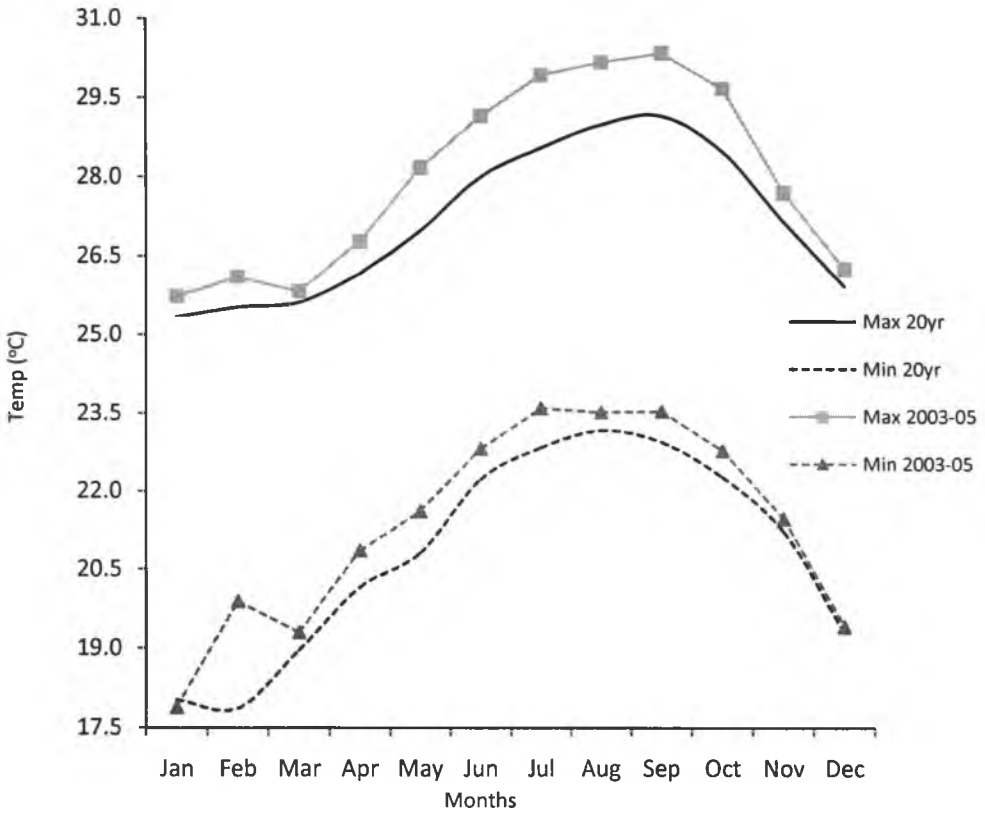

Figure 2.3. Average maximum and minimum temperature at Waimanalo from 2003 to 2005 and 20 year period (1980-2000).

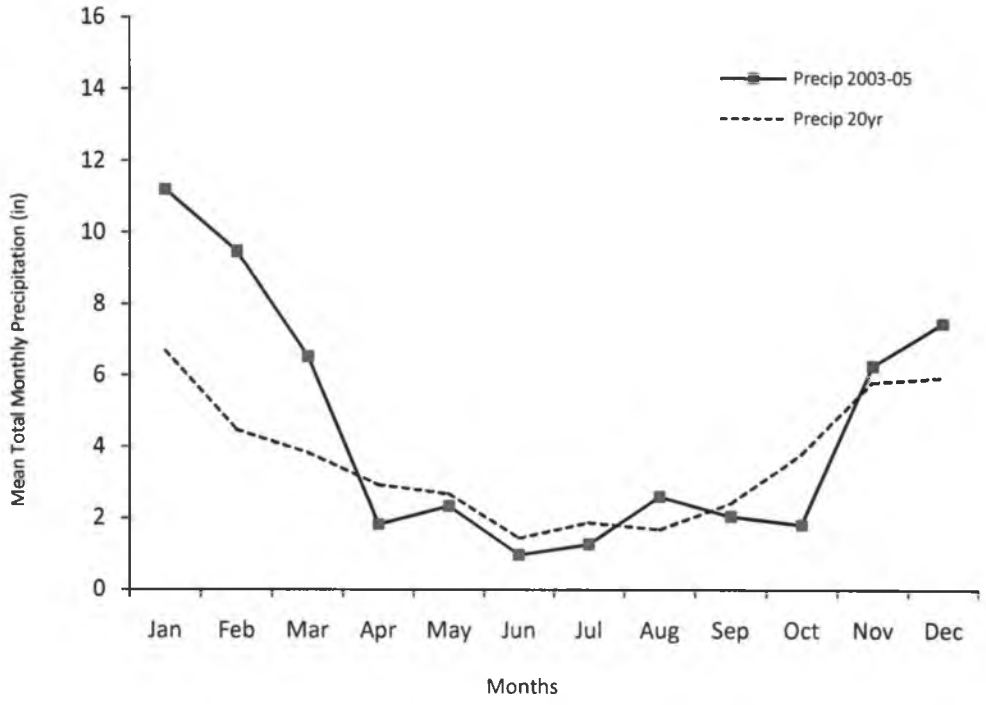

Figure 2.4. Comparison of average monthly precipitation from 2003-2005 and 20 year period (1980-2000) at Waimanalo, Hawaii.

Grain filling rate and grain filling periods were taken from the 8 inbreds and 28 hybrids in the diallel plantings on August 2004 (cool, low PAR), March and May 2005 (hot, high PAR).

2.2.2 Maize inbred lines

Eight tropically adapted maize inbred lines (Table 2.1) bred in different research institutions were used in this study. They are elite inbreds that are widely used in hybrids and that range greatly in origin (tropical, temperate) and type (dent, flint). These inbreds have been grown and converted for resistance to several tropical diseases at the Waimanalo Research Station of the University of Hawaii (Brewbaker, 1997; Brewbaker and Josue, 2007).

Table 2.1. Selected maize inbred lines for diallel analysis.

Inbred	Source	Origin	Seed type	Breeder
Hi26	Hi26	CM202 (=CI21E)	Southern dent	Brewbaker
Hi53	ICA L210	Cuban Flint 5832#	Tropical flint	Arboleda
Hi57	Ki9	Suwan 1(S)C4 (=KU1409)	Tropical flint	Sujin/ Sutat
Hi60	Mo17	CI187-2 x C103	Corn belt dent	Zuber
Hi61	N3y	White dents (=SR52F)	Southern dent	Nelson
Hi62	Pi17	Tropical x Temp	Tropical flint	Logroño
Hi65	Tx601	Yellow Tuxpan	Tropical dent	Bockholt
Hi67	Tzi18	SeteLagaos TZSR x 7729	Tropical flint	Kim

2.2.3 Diallel entries

The eight inbreds were crossed in diallel manner excluding reciprocals (Griffing 1956, Method 2) during the Fall of 2003 and Spring of 2004 at the Waimanalo Research

Station (20° N latitude). Each inbred was used as either a male or female and the F1 seeds were bulked at harvest. The 28 F_1 crosses and two single cross augments, H1086, H1090 and the 8 inbred parents were evaluated in a modified randomized complete block with two replications. Crosses and parents were grouped separately within the same block and randomized separately within groups. Hybrid H1035 and inbred Hi43 were used as the hybrid and inbred borders, respectively.

Complete fertilizer was applied as a basal application a day prior to planting at a rate of 160 kg of N and 80 kg of P_20_5 and K_2O per hectare. Alachlor and Atrazine were applied as pre-emergence herbicides immediately after planting. Whenever necessary, post emergence herbicides such as glyphosate and 2,4-D were also applied at tasseling. Trials were irrigated using a drip tube system.

Entries were grown in two rows 5 m long spaced 0.75 m apart (7.5 m^2). Two to three seeds were planted per hill using a hand jab planter at 0.25 m spacing and thinned to one plant (53,333 plants per hectare) at around the 5-8 leaf stage.

Diallel entries were grown and evaluated in a series of plantings that began in July and August of 2004, and continued in March and May of 2005.

2.2.4 Traits measured

The primary traits considered in this study included grain filling rate, grain filling period, and chlorophyll readings (SPAD). The following traits were recorded from each plot:

1. *Grain filling rate (GFR)* - Five ears from the inner plots were randomly sampled at 14 days after mid-silk (50% of plants in a plot emerged silk). Harvesting was continued at 21, 28 and 36 days after mid-silk and one final harvest at maturity (total plant dry down). Harvested ears were dried in a cabinet-type drier at room temperature (25-27°C) for 7 days. The kernels were shelled and dried further at 70°C for one week or to constant weight. A total of 100 kernels were sampled and weighed from each ear. Grain filling rate was calculated as the slope of the linear regression of kernel dry weight and time.

2. *Grain filling period* – This was determined by dividing the final kernel weight by the grain filling rate, a procedure described previously by Daynard (1971). This is also known as the effective filling period duration (EFPD).

3. *Chlorophyll readings (SPAD)* – This was determined using a Minolta SPAD 502 (Spectrum Technologies, Plain-Field, IL) instrument. Chlorophyll readings were taken at three different growth stages, 30, 60 and 90 days after planting. Measurements were taken from the youngest leaf on one side of the midrib halfway between the base and the tip and from a random sample of 10 plants per plot.

4. *Days to mid-anthesis and mid-silk* – the number of days from planting to time when 50% of the plants have shed pollen and emerged silk, respectively.

5. *Plant and ear height (cm)* – average measurement of 10 randomly selected plants per plot measured from the base of the plant to the node of the flag leaf for plant height, and from the base of the plant to the node bearing the upper most ear for ear height.

6. *Ear length and diameter (cm)* - average length of 5 randomly chosen ears measured from the base to the tip of the ear for ear length, and from side to side of the ear for ear diameter, respectively.

7. *Plant yield (g)* – Mean weight of 5 randomly harvested mature ears dried to approximately 12.0% moisture.

8. *Kernel weight (g)* - weight of a bulk of 100 kernels per ear from 5 randomly selected ears per plot.

9. *Kernel density* (g^{-1} cm^{-3}) – calculated by dividing 500 kernel weight by the volume. Kernel volume was determined by water displacement using a graduated cylinder.

2.2.5 Analysis of variance for traits

The analyses of variance for individual and combined Waimanalo planting dates were conducted for each trait using the PROC GLM Procedure of SAS (SAS Institute, 1996) and Brewbaker (2003). For the diallel trial, entries were partitioned into variation among inbred parents, F_1's and parents vs. F_1's. Entries by month interactions were also

tested. Table 2.2 shows the format for the analysis of variance and the expectation of mean squares.

Table 2.2. Format of the analysis of variance and the expected mean squares.

Source	df	Expected mean squares
Months (M)	3	$\sigma^2_e + r\sigma^2_{Mt} + rM\,\theta_t$
Rep (Months) (r/M)	4	$\sigma^2_e + t\sigma^2_{M\,t} + rM\,\theta_t$
Entries (t)	35	$\sigma^2_e + r\sigma^2_{Mt} + rM\,\theta_t$
Inbreds	7	
Hybrids	27	
Inbreds vs. Hybrids	1	
Entry x Month	105	$\sigma^2_e + r\sigma^2_{M\,t}$
Inbreds x M	21	
Hybrids x M	81	
Inbreds vs. Hybrids x M	3	
Pooled error	137	σ^2_e
Total	284	

The model used for the analysis of variance is as follows.

$$Y_{ijkl} = \mu + \alpha_l + \beta_{k(l)} + \tau_i + (\alpha\,\tau)_{il} + \varepsilon_{ijkl}$$

Where; μ = grand mean
α_l = month effect
$\beta_{k(l)}$ = reps within months effect
τ_i = genotype effects
$(\alpha\,\tau)_{il}$ = genotype by month interaction
ε_{ijkl} = experimental error

2.2.6. Mid-parent heterosis

Mid-parent heterosis was calculated by subtracting the mean of the inbred parents from the F1 hybrid mean and expressed as percentage.

2.2.7 Analysis of variance for general and specific combining ability

Diallel analysis was conducted using Method 2, Model 1 (Griffing, 1956). Calculations were performed on MS Excel software spreadsheet according to the procedures outlined by Brewbaker (2003). Table 2.3 shows the format of the ANOVA, and expected mean squares used in this analysis.

The genetic model used for the analysis of combining ability is as follows;

$Y_{ijl} = \mu + g_i + s_{ij} + g_{il} + s_{ijl} + e_{ijkl}$

Where μ = mean

$g_{i,}$ = general combining ability of inbred line

s_{ij} = specific combining ability between inbreds i and j

g_{il} = general combining ability x month interaction

s_{ijl} = specific combining ability x month interaction

e_{ijl} = experimental error

Where, g_i, s_{ij} are fixed and g_{iL} and s_{ijL} are random.

Table 2.3. Format of the analysis of variance used in the diallel analysis and expected mean squares.

Source	df	MS	Expected mean squares
Combining ability			
GCA (g)	p-1	M5	$\sigma^2_e+r\sigma^2_{sM}+(p+2)\sigma^2_{gM}+M(P+2)\theta_g$
SCA (s)	p(p-1)/2	M4	$\sigma^2_e+r\sigma^2_{sM}+M\theta_s$
Interaction			
GCA x M (g x M)	(p –1) (E –1)	M3	$\sigma^2_e+r\sigma^2_{sM}+(p+2)\sigma^2_{gM}$
SCA x M (s x M)	p(p-1) (E-1)/2	M2	$\sigma^2_e+r\sigma^2_{sM}$
Error (e)	E(v –1) (r –1)	M1	σ^2_e

2.3 Results

2.3.1 Grain filling rate

2.3.1.1 Mean performance and analysis of variance

Mean GFR among inbreds in the three tested planting dates was 8.41 mg k^{-1} day^{-1} (Table 2.4). Among inbreds, GFR was slowest in the 8/04 planting (7.51 mg k^{-1} day^{-1}), and the fastest in the 3/05 (9.24 mg k^{-1} day^{-1}) followed by the 5/05 planting (8.48 mg k^{-1} day^{-1}). Grain filling rate was slowest for Hi65 (6.86 mg k^{-1} day^{-1}) and fastest for Hi61 (10.21 mg k^{-1} day^{-1}) based on the means across planting dates. Inbreds Hi61 and Hi53 achieved the highest GFR values, 10.21 and 9.96 mg k^{-1} day^{-1}, respectively. The fastest filling inbred in the 8/04 planting was Hi53 that filled at a rate of 10.08 mg k^{-1} day^{-1}, while slowest filling inbred in this same month was Hi60 (5.71 mg k^{-1} day^{-1}). These two inbreds were selected as parents to form populations for generation mean analysis (Chapter 3).

Mean GFR of the 28 hybrids (Table 2.4) was 10.05 mg k^{-1} day^{-1}. The slowest occurred in the 8/04 planting (9.17 mg k^{-1} day-1), followed by the 3/05 (10.38 mg k^{-1} day^{-1}) and 5/05 (10.60 mg k^{-1} day^{-1}) plantings. Mean F1 performance ranged from 8.31 mg k^{-1} day^{-1} for Hi65 x Hi67 to 12.02 mg k^{-1} day^{-1} for hybrid Hi61 x Hi62. Hybrids that also had comparable high GFR were Hi53 x Hi61 and Hi57 x Hi61, which filled at a rate of 11.42 and 11.41 mg k^{-1} day^{-1}, respectively. Hybrid Hi61 x Hi62 was the fastest filling hybrid in the 8/04 (12.17 mg k^{-1} day^{-1}) and 3/05 (12.5 mg k^{-1} day^{-1}) plantings. For the 5/05 planting, Hi60 x Hi61 was the fastest filling hybrid (13.36 mg k^{-1} day^{-1}), followed

Table 2.4. Mean GFR within and across Waimanalo planting dates.

Entry	Pedigree	GFR (mg k^{-1} day^{-1})				MPH*
		8/04	3/05	5/05	Mean	(%)
Inbreds						
Hi53	ICAL210	10.08	10.61	9.19	9.96	
Hi57	Ki9	7.96	7.97	8.73	8.22	
Hi60	Mo17	5.71	9.24	8.42	7.79	
Hi61	N3y	7.57	11.96	11.11	10.21	
Hi62	Pi17	8.33	8.56	8.07	8.32	
Hi65	Tx601	6.00	8.23	6.34	6.86	
Hi67	Tzi18	6.90	6.70	7.17	6.92	
Hi26	Hi26	7.52	10.64	8.84	9.00	
Inbred means		7.51	9.24	8.48	8.41	
$LSD_{0.05}$ Inbreds		2.34	1.42	1.81	1.89	
Hybrids						
Hi53 x Hi57	ICAL210 x Ki9	10.33	10.08	9.92	10.11	10.10
Hi53 x Hi60	ICAL210 x Mo17	10.87	10.24	12.05	11.05	19.70
Hi53 x Hi61	ICAL210 x N3y	10.76	11.37	12.13	11.42	11.66
Hi53 x Hi62	ICAL210 x Pi17	11.32	10.44	10.15	10.64	14.08
Hi53 x Hi65	ICAL210 x Tx601	10.13	9.14	10.71	9.99	15.86
Hi53 x Hi67	ICAL210 x Tzi18	9.78	10.06	10.26	10.03	15.88
Hi53 x Hi26	ICAL210 x Hi26	9.69	11.12	10.56	10.46	9.33
Hi57 x Hi60	Ki9 x Mo17	9.53	10.30	10.60	10.14	21.10
Hi57 x Hi61	Ki9 x N3y	10.89	11.00	12.36	11.41	19.26
Hi57 x Hi62	Ki9 x Pi17	8.52	9.79	9.44	9.25	10.62
Hi57 x Hi65	Ki9 x Tx601	8.48	9.14	9.21	8.94	15.73
Hi57 x Hi67	Ki9 x Tzi18	10.15	10.16	9.39	9.90	23.52
Hi57 x Hi26	Ki9 x Hi26	11.22	10.72	11.22	11.05	22.11
Hi60 x Hi61	Mo17 x N3y	8.01	12.03	13.36	11.14	19.16
Hi60 x Hi62	Mo17 x Pi17	9.06	10.08	10.99	10.04	19.81
Hi60 x Hi65	Mo17 x Tx601	5.70	9.81	9.91	8.47	13.56
Hi60 x Hi67	Mo17 x Tzi18	7.12	10.34	11.38	9.61	23.48
Hi60 x Hi26	Mo17 x Hi26	4.70	9.64	11.51	8.62	2.56
Hi61 x Hi62	N3y x Pi17	12.17	12.50	11.39	12.02	22.89
Hi61 x Hi65	N3y x Tx601	8.23	11.62	10.56	10.14	15.80
Hi61 x Hi67	N3y x Tzi18	10.45	10.98	12.65	11.36	24.59
Hi61 x Hi26	N3y x Hi26	8.47	12.01	11.71	10.73	10.46
Hi62 x Hi65	Pi17 x Tx601	9.80	9.96	8.50	9.42	19.43
Hi62 x Hi67	Pi17 x Tzi18	8.44	9.55	9.28	9.09	16.17
Hi62 x Hi26	Pi17 x Hi26	8.97	10.70	9.38	9.68	10.57
Hi65 x Hi67	Tx601 x Tzi18	6.69	9.29	8.95	8.31	17.10
Hi65 x Hi26	Tx601 x Hi26	7.16	8.88	9.18	8.41	5.68
Hi67 x Hi26	Tzi18 x Hi26	10.11	9.58	10.10	9.93	19.81
Hybrid means		9.17	10.38	10.60	10.05	16.07
$LSD_{0.05}$ Hybrids		1.73	1.70	1.52	1.65	
Grand mean		8.80	10.12	10.13	9.68	

*MPH=mid parent heterosis(%)

by Hi61 x Hi67 (12.65 mg k^{-1} day^{-1}), Hi57 x Hi61 (12.36 mg k^{-1} day^{-1}), and Hi53 x Hi61 (12.13 mg k^{-1} day^{-1}). Hybrid Hi60 x Hi26 filled at a rate of 4.70 mg k^{-1} day^{-1}, which was the slowest in the 8/04 planting. Hybrids, Hi65 x Hi26 and Hi62 x Hi65 also had slow filling during in the 3/05 and 5/05 planting dates, respectively.

Hybrids consistently exceeded inbreds in grain filling rate (Table 2.4). Mid-parent heterosis (MPH, %) was calculated by subtracting the mean of the parents from their hybrid means using the data across planting dates. MPH values averaged 164% and ranged from 279% (Hi61 x Hi67) to 22% (Hi60 x Hi26). Hybrids Hi61 x Hi62 and Hi61 x Hi67 had comparably high MPH values of 257% and 279%.

Inbred performances were highly correlated with their corresponding hybrid array means and all were statistically significant (Table 2.5). The hybrid array means across planting dates were highest for Hi61 (11.17 mg k^{-1} day^{-1}), followed by Hi53 (10.53 mg k^{-1} day^{-1}) and the least for Hi65 (9.10 mg k^{-1} day^{-1}). The hybrid array means were consistently higher for Hi61, which were 11.65 and 12.02 mg k^{-1} day^{-1}, for the 3/05 and 5/05 plantings, respectively. In the 8/04 trial, Hi53 had the highest array mean (10.41 mg k^{-1} day^{-1}) compared to Hi61 (9.85 mg k^{-1} day^{-1}). Correlation analyses between inbred per se and hybrid performances for GFR were performed. The correlation coefficient (r) (Table 2.5) was highest in the 8/04 planting (r=0.903, P<0.01), followed by the 5/05 (r=0.838, P<0.01) and 3/05 plantings (r=0.772, P<0.01). Across planting dates, the correlation between inbred and hybrid performance was 0.876 (P<0.01).

Analyses of variance for GFR for the three plantings are presented on Table 2.6. Variation was highly significant among inbreds (P<0.01) and hybrids (P<0.01) in all the

Table 2.5. Comparison and correlation between inbred means and array means for GFR within individual Waimanalo planting dates.

	Inbred means				Array means			
Inbred	8/04	3/05	5/05	Mean	8/04	3/05	5/05	Mean
Hi53	10.08	10.61	9.19	9.96	10.41	10.35	10.82	10.53
Hi57	7.96	7.97	8.73	8.22	9.87	10.17	10.31	10.12
Hi60	5.71	9.24	8.42	7.79	7.86	10.35	11.40	9.87
Hi61	7.57	11.96	11.11	10.21	9.85	11.65	12.02	11.17
Hi62	8.33	8.56	8.07	8.32	9.76	10.43	9.88	10.02
Hi65	6.00	8.23	6.34	6.86	8.02	9.69	9.57	9.10
Hi67	6.90	6.70	7.17	6.92	8.96	9.99	10.29	9.75
Hi26	7.52	10.64	8.84	9.00	8.62	10.38	10.52	9.84
Mean	7.51	9.24	8.48	8.41	9.17	10.38	10.60	10.05
Correlation coefficients					0.903 **	0.772 *	0.838 **	0.876 **

Table 2.6. Mean squares for GFR among individual Waimanalo planting dates.

Source	df	Planting dates		
		8/04	3/05	5/05
Entries	35	6.53 **	3.00 **	4.79 **
Inbreds	7	3.83 **	5.95 **	4.02 **
Hybrids	27	6.21 **	1.74 **	3.10 **
I vs H	1	34.28 **	16.13 **	55.86 **
Reps	1	2.69 ns	0.07 ns	0.35 ns
Error	35	0.67	0.51	0.53
Total	71			
CV%		9.3%	7.1%	7.2%
Grand mean		8.80	10.12	10.13

planting dates. Heterosis as revealed by the comparison of inbreds versus hybrids were also significant ($P<0.01$) in all the planting dates. Replication variations were not significant, a reflection of the homogeneity of Waimanalo corn plots that had been consistently grown to corn since the 1960's. Coefficients of variation were very low, ranging from 7.1% to 9.3%, maximized in the autumn (8/04), low-light trial.

Analyses of variance for GFR (Table 2.7) revealed highly significant differences among planting dates ($P<0.01$). The replications within planting dates were not significant, consistent with the individual ANOVAs. Variation among the inbreds and hybrids were significant ($P<0.01$) as was heterosis ($P<0.0001$). Highly significant differences were found for genotype x month interactions and for interactions among inbreds and hybrids with the planting dates. It was clear that the autumn planting (8/04) produced significantly lower GFR values for all entries, leading both to a highly significant month effect but to the high genotype x month interactions. The greatly reduced temperatures and PAR values of this planting (Figures 2.1, 2.2) evidently accounted for these observations.

2.3.1.2 Diallel analysis for grain filling rate

Diallel analysis was conducted to estimate general combining ability (GCA) and specific combining ability (SCA) effects for grain filling rate, grain filling period, chlorophyll concentration and other agronomic characters. General combining ability effects is a measure of additive gene effects, while SCA is a measure or non-additive

Table 2.7. ANOVA for GFR across Waimanalo planting dates.

Source	df	SS	MS	F	$F_{0.05}$	$F_{0.01}$
Months	2	84.49	42.25	40.84 **	3.09	4.82
Reps in Months	4	3.10	1.03	1.81 ns	2.69	3.98
Genotypes	35	330.76	9.45	3.88 **	1.54	1.84
Inbreds	7	66.41	9.49	4.40 **	2.10	2.82
Hybrids	27	164.07	6.08	2.45 **	1.60	1.93
I vs H	1	100.28	100.28	33.49 ****	3.93	6.89
Entry x Month	70	170.34	2.43	4.25 **	1.43	1.66
Inbreds x M	14	30.18	2.16	3.77 **	1.79	2.26
Hybrids x M	54	134.17	2.48	4.34 **	1.46	1.71
(I vs H) x M	2	5.99	2.99	5.23 **	3.09	4.82
Pooled Error	102	58.37	0.57			
Total	212	647.08				

CV %	7.81%
$LSD_{0.05}$ Inbreds	1.89
$LSD_{0.05}$ Hybrids	1.65

gene effects. Diallel analysis was based on Griffing's (1956) Method 2, Model 1 (Fixed Effects Model) analysis, which included the parents without the reciprocal crosses.

The analyses of GCA and SCA effects on the 28 F1 hybrids for GFR were conducted across the three Waimanalo planting dates (Table 2.8), providing values of mg k^{-1} day^{-1}. For the combined analysis of GCA effects (Table 2.8a), Hi61 had the highest GCA (0.86), followed by Hi53 (0.48). The lowest GCA was -0.73 of Hi65. General combining ability effects were consistently high for Hi61 in all three trials. High GCA effects were also observed in Hi53 in all three planting dates, while GCA was negative and large for Hi65 in all trials. For the analysis of SCA effects, Hi60 x Hi26 was observed to have the lowest SCA (-0.59), while Hi57 x Hi26 the highest (1.04). Hybrids with higher SCA effects also included Hi61 x Hi62 (0.92), Hi61 x Hi67 (0.78), Hi53 x Hi60 (0.53) and Hi57 x Hi26 (0.59).

General and specific combining ability effects varied within individual planting dates. For the trial planted in 8/04 (Table 2.8b), GCA effects (in bold, below diagonal) were lowest for Hi60 (-1.28) and highest for Hi53 (1.38). Both Hi57 and Hi62 had the same GCA effect (0.58) which was then followed by Hi61 (0.49). For the SCA analysis, lowest SCA effect was obtained by Hi60 x Hi26 (-2.44) while the highest was Hi61 x Hi62 (2.30). Five inbreds that were crossed to Hi26 had negative SCA values but hybrid Hi57 x Hi26 gave a high SCA (2.22) followed by Hi67 x Hi26 (1.96). Other high SCAs characterized Hi53 x Hi60 (1.96) and Hi62 x Hi65 (1.52).

General combining ability effects for GFR in the trial planted in 3/05 (Table 2.8c) were highest for Hi61 (1.43) followed by Hi26 (0.28), Hi53 (0.26), and Hi60 (-0.02).

Table 2.8. GCA effects (below diagonal) and SCA effects for GFR within and across Waimanalo planting dates.

(a) - Combined

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**0.48**	-0.17	0.73	-0.05	0.26	0.48	0.16	0.12
Hi57		**0.01**	0.53	0.43	-0.30	0.17	0.53	1.04
Hi60			**-0.19**	0.41	0.49	0.01	0.52	-0.59
Hi61				**0.86**	0.92	0.21	0.78	-0.06
Hi62					**-0.03**	0.56	-0.04	0.05
Hi65						**-0.73**	0.08	-0.20
Hi67							**-0.38**	0.59
Hi26								**-0.02**

(b) - 8/04

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**1.38**	-0.44	1.96	0.08	0.56	1.05	-0.13	-0.11
Hi57		**0.58**	1.43	1.01	-1.44	0.20	1.03	2.22
Hi60			**-1.28**	-0.0005	0.97	-0.72	-0.13	-2.44
Hi61				**0.49**	2.30	0.04	1.43	-0.44
Hi62					**0.58**	1.52	-0.67	-0.02
Hi65						**-1.10**	-0.74	-0.16
Hi67							**-0.27**	1.96
Hi26								**-0.38**

(c) - 3/05

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**0.26**	0.10	-0.12	-0.44	0.16	-0.56	0.46	0.46
Hi57		**-0.40**	0.59	-0.16	0.16	0.10	1.21	0.71
Hi60			**-0.02**	0.49	0.07	0.39	1.01	-0.74
Hi61				**1.43**	1.04	0.75	0.20	0.17
Hi62					**-0.10**	0.61	0.30	0.39
Hi65						**-0.68**	0.62	-0.85
Hi67							**-0.78**	-0.05
Hi26								**0.28**

(d) - 5/05

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**0.30**	-0.35	1.08	0.18	0.31	1.43	0.31	0.12
Hi57		**-0.16**	0.08	0.86	0.06	0.39	-0.10	1.23
Hi60			**0.55**	1.17	0.90	0.38	1.18	0.82
Hi61				**1.52**	0.33	0.06	1.48	0.04
Hi62					**-0.59**	0.11	0.23	-0.17
Hi65						**-1.15**	0.45	0.19
Hi67							**-0.48**	0.43
Hi26								**0.02**

Inbred Hi67 had the lowest GCA effect (-0.78). For SCA effects, Hi65 x Hi26 had the lowest SCA (-0.85), while Hi57 x Hi67 the highest (1.21). This was then followed by hybrids Hi62 x Hi61 and Hi60 x Hi67, which had SCA effects of 1.04 and 1.01, respectively.

For the trial planted on 5/05, Hi61 remained the highest combiner (1.52), followed by Hi60 (0.55) and Hi53 (0.30) (Table 2.8d). The inbred with the lowest GCA effect was Hi65 (-1.15). Among the hybrids, SCA effects for GFR ranged from -0.35 (Hi53 x Hi57) to 1.48 (Hi61 x Hi67). Other high SCA combinations were Hi53 x Hi65 (1.43), Hi57 x Hi26 (1.23) and Hi60 x Hi61 (1.17).

Magnitudes of GCA effects were consistent for some inbreds between planting dates (Figure 2.4). Inbreds Hi53 and Hi61 consistently increased grain filling rates (GCA > 0.00) despite temperature and PAR differences between the three Waimanalo planting dates (Figures 1.1, 1.2, Chapter 2). Inbred Hi61 was originally bred and adapted to the lower temperatures and longer periods of light in the tropical highlands of Zimbabwe. This may explain the fact that it filled faster under related conditions in the 3/05 and 5/05 Waimanalo planting dates. Similarly inbred Hi60 reduced grain filling rates in 8/04 under inadequate PAR and low temperature, and increased GFR in 3/05 and 5/05 under high PAR and temperature. Inbred Hi60, a temperate dent (Mo17) was originally bred for short planting dates and is the earliest maturing. In contrast inbreds Hi65 and Hi67 slowed down grain filling rates (GCA < 0.00) in all three planting dates.

Analyses of variance for GCA and SCA effects were also conducted across the three Waimanalo planting dates (Table 2.9). The relative importance of GCA and SCA

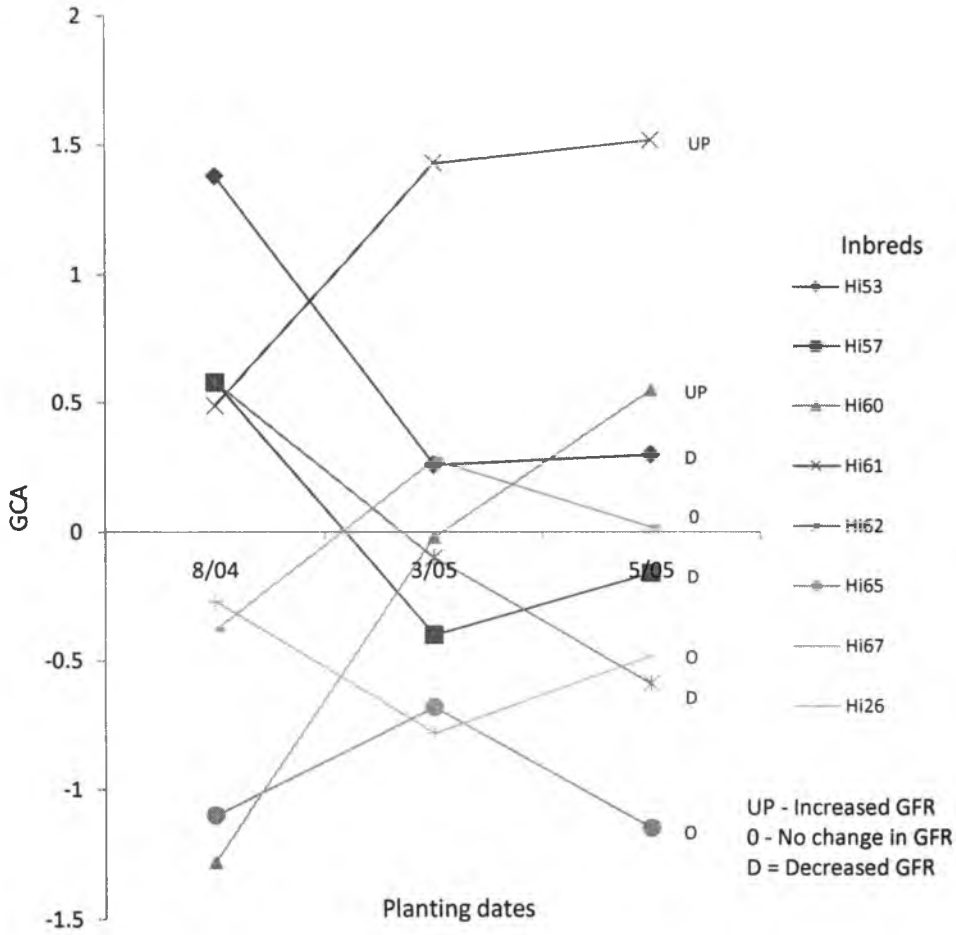

Figure 2.5. General combining ability x month interaction for GFR.

Table 2.9. Mean squares for combining ability for GFR within individual Waimanalo planting dates.

Source	df	Planting dates		
		8/04	3/05	5/05
GCA	7	8.43 **	4.91 **	6.60 **
SCA	20	2.77 **	0.90 **	1.88 **
Error	35	0.34	0.26	0.26
Ratio				
2GCA/(2GCA+SCA)		0.86	0.92	0.88
GCA:SCA		3.05	5.44	3.51

effects were assessed using the mean square ratios of GCA to SCA, following the formulas of Baker (1978). Both GCA and SCA effects were found to be highly significant for the three trials. The simple mean square ratios of GCA to SCA were 3.05, 5.44, 3.51 for the trials 8/04, 3/05 and 5/05, respectively, showing GCA effects to prevail over SCA effects in these planting dates.

The combined analysis of variance for the three trials is presented in Table 2.10. SCA effects were highly significant ($P<0.01$) while GCA effects were not significant. The simple ratio of GCA to SCA mean squares was 4.83 showing greater contributions of additive gene effects. The modified GCA to SCA ratio of Baker (1978) was only 0.87. Both interactions of GCA and SCA by month were significant ($P<0.01$) for GFR (Table 2.10).

Table 2.10. Analysis of variance for combining ability effects for GFR across Waimanalo planting dates.

Source	df	SS	MS	F	$F_{0.05}$	$F_{0.01}$
GCA	7	67.83	9.69	1.890 ^{ns}	2.764	4.278
SCA	28	56.21	2.01	2.053 *	1.678	2.078
GCA x M	14	71.76	5.13	17.912 **	1.790	2.262
SCA x M	56	54.76	0.98	3.417 **	1.458	1.703
Error	102	29.19	0.29			
Ratio						
GCA:SCA		4.83				
2GCA/(2GCA+SCA)		0.87				

2.3.2 Grain filling period

2.3.2.1 Mean performance and analysis of variance

The GFP values in this study were calculated as the effective filling period duration (EFPD) as defined by Johnson and Tanner (1972). This was estimated by dividing the final kernel weight at maturity by the corresponding grain filling rate of the inbred or hybrid. The final harvest was done when the plants were fully dried down to ensure physiological maturity, around 42 days after silking.

Mean GFP among inbreds across planting dates was 31.9 days (Table 2.11). The shortest GFP was observed among inbreds grown during the 8/04 planting (27.1 days) compared to the 3/05 (32.7 days) and 5/05 (35.7 days) planting dates. Across planting dates, the mean GFP ranged from 26.2 days (Hi26) to 35.5 days (Hi57). Inbreds Hi62 and Hi57 had the shortest (23.9 days) and longest (34.4 days) GFP, respectively in the 8/04 trial. These inbreds were selected as parents to form the populations for generation mean analysis of GFP. In the 3/05 trial, Hi57 remained the inbred with the longest filling period (35.60 days). The shortest filling inbred at this planting month was Hi26 (26.75 days). In the 5/05 planting, inbred Hi65 had the longest GFP followed by Hi57, but the difference between these inbreds was not significant. Inbred Hi26 continued to be the shortest filling in this month.

Mean GFP among the 28 F1 hybrids across planting dates was 32.4 days (Table 2.11). The GFP among hybrids was shortest during the 8/04 planting (27.3 days), and longer in the 3/05 (33.7) and 5/05 (36.3) plantings, obviously correlated with light and temperature differences. Across planting dates, mean GFP was shortest for Hi53 x Hi60

Table 2.11. Mean GFP within individual and across Waimanalo planting dates.

Entry	Pedigree	GFP (Days)				MPH**
		8/04	3/05	5/05	Mean	(%)
Inbreds						
Hi53	ICAL210	27.56	29.30	33.06	29.97	
Hi57	Ki9	34.42	35.60	35.92	35.31	
Hi60	Mo17	25.99	27.32	34.67	29.33	
Hi61	N3y	25.32	29.00	34.15	29.49	
Hi62	Pi17	23.91	29.15	32.22	28.43	
Hi65	Tx601	28.41	27.46	36.60	30.82	
Hi67	Tzi18	25.05	29.79	32.19	29.01	
Hi26	Hi26	19.84	26.75	32.09	26.22	
Inbred means		26.31	29.30	33.86	29.82	
$LSD_{0.05}$ Inbreds		9.97	4.65	7.49	7.68	
Hybrids						
Hi53 x Hi57	ICAL210 x Ki9	32.61	34.63	37.46	34.90	6.46
Hi53 x Hi60	ICAL210 x Mo17	20.73	34.16	30.52	28.47	-4.15
Hi53 x Hi61	ICAL210 x N3y	25.44	37.19	37.45	33.36	10.88
Hi53 x Hi62	ICAL210 x Pi17	28.27	37.17	39.68	35.04	16.67
Hi53 x Hi65	ICAL210 x Tx601	28.98	39.42	34.96	34.45	11.77
Hi53 x Hi67	ICAL210 x Tzi18	29.10	32.73	36.40	32.74	9.93
Hi53 x Hi26	ICAL210 x Hi26	27.61	33.27	37.00	32.63	13.88
Hi57 x Hi60	Ki9 x Mo17	29.48	28.99	32.45	30.31	-6.64
Hi57 x Hi61	Ki9 x N3y	32.50	34.67	34.41	33.86	4.30
Hi57 x Hi62	Ki9 x Pi17	33.11	34.35	38.44	35.30	9.72
Hi57 x Hi65	Ki9 x Tx601	32.29	34.33	37.41	34.68	4.63
Hi57 x Hi67	Ki9 x Tzi18	26.42	29.70	36.32	30.81	-4.37
Hi57 x Hi26	Ki9 x Hi26	26.87	34.00	36.27	32.38	4.97
Hi60 x Hi61	Mo17 x N3y	26.76	34.52	34.50	31.93	7.88
Hi60 x Hi62	Mo17 x Pi17	26.74	35.08	36.71	32.84	12.06
Hi60 x Hi65	Mo17 x Tx601	23.63	30.42	32.29	28.78	-4.50
Hi60 x Hi67	Mo17 x Tzi18	25.84	28.34	32.43	28.87	-1.03
Hi60 x Hi26	Mo17 x Hi26	33.18	36.35	33.81	34.45	19.37
Hi61 x Hi62	N3y x Pi17	22.54	34.65	40.32	32.51	10.91
Hi61 x Hi65	N3y x Tx601	24.11	33.14	39.78	32.35	6.77
Hi61 x Hi67	N3y x Tzi18	24.44	32.39	31.61	29.48	0.78
Hi61 x Hi26	N3y x Hi26	23.24	33.15	36.48	30.95	10.01
Hi62 x Hi65	Pi17 x Tx601	28.06	34.93	43.88	35.62	16.83
Hi62 x Hi67	Pi17 x Tzi18	28.31	32.35	35.16	31.94	10.08
Hi62 x Hi26	Pi17 x Hi26	25.65	32.85	39.98	32.83	16.76
Hi65 x Hi67	Tx601 x Tzi18	30.89	30.67	35.26	32.27	7.30
Hi65 x Hi26	Tx601 x Hi26	25.27	36.69	38.94	33.63	15.19
Hi67 x Hi26	Tzi18 x Hi26	23.73	33.60	36.19	31.17	11.40
Hybrid means		27.35	33.71	36.29	32.45	7.78
$LSD_{0.05}$ Hybrids		7.52	6.22	5.40	6.44	
Grand mean		27.12	32.73	35.75	31.86	

**MPH=mid parent heterosis(%)

(28.47 days) and the longest included Hi62 x Hi65 (35.62 days), and Hi57 x Hi62 (35.0 days). The GFP responses of some hybrids varied across Waimanalo planting dates. In the 8/04 planting (Table 2.11), the longest and shortest filling hybrids were Hi57 x Hi62 (33.1 days) and Hi53 x Hi60 (20.7 days), respectively. For the 3/05 trial, the hybrid with the longest GFP was Hi53 x Hi65 (39.4 days) and shortest was Hi60 x Hi67 (28.3 days). The longest filling hybrid for the 5/05 planting was Hi62 x Hi65 (43.9 days) followed by Hi61 x Hi62 (40.3 days). The hybrid with the shortest GFP was Hi53 x Hi60 (30.52 days), a hybrid that was also the shortest filler (20.73) in the 8/04 month.

Mid-parent heterosis values were calculated for GFP using the mean GFP values across planting dates (Table 2.11). MPH averaged 262% and ranged from -201% to 667% observed for hybrids Hi57 x Hi60 and Hi60 x Hi26, respectively. Hybrids that had negative MPH values indicate that the GFP of the F_1 hybrid was less than the mean GFP of their parents, an expression of heterosis for short grain fill periods. Only 5 of the 28 hybrids had negative MPH values for GFP (Table 2.11). As observed for GFR values, the mean values for GFP were lowest in the cool, shady autumn days of the 8/04 trial.

The inbred means were also compared with their corresponding hybrid array means (Table 2.12). Hybrid array means for GFP in the trial planted in 8/04 ranged from 25.6 days for Hi61 to 30.5 days for Hi57. For the trial in 3/05, Hi67 (31.4 days) and Hi53 (35.5), were the shortest and longest filling inbreds, respectively. For the trial in 5/05, hybrid array means for GFP were lowest for Hi60 (33.2) and highest for Hi62 (39.2). Finally, for the combined data of the hybrid array means across planting dates, Hi60 (30.8) was the shortest filling while Hi62 was the longest (33.7) filling.

Table 2.12. Comparison of inbred means and array means for GFP within individual Waimanalo planting dates.

	Inbred means				Array means			
Inbred	8/04	3/05	5/05	Mean	8/04	3/05	5/05	Mean
Hi53	27.56	29.30	33.06	29.97	27.53	35.51	36.21	33.08
Hi57	34.42	35.60	35.92	35.31	30.47	32.95	36.11	33.18
Hi60	25.99	27.32	34.67	29.33	26.62	32.55	33.24	30.81
Hi61	25.32	29.00	34.15	29.49	25.58	34.24	36.36	32.06
Hi62	23.91	29.15	32.22	28.43	27.52	34.48	39.17	33.73
Hi65	28.41	27.46	36.60	30.82	27.61	34.23	37.50	33.11
Hi67	25.05	29.79	32.19	29.01	26.96	31.40	34.77	31.04
Hi26	19.84	26.75	32.09	26.22	26.51	34.27	36.95	32.58
Mean	26.31	29.30	33.86	29.82	27.35	33.71	36.29	32.45
Correlation coefficients					0.801 *	-0.247 ns	-0.127 ns	0.239 ns

The correlation coefficients were also calculated between inbred and hybrid performance for GFP (Table 2.12). In 8/04, the *r* was significant ($r = 0.801$, $P<0.05$). In the 3/05 and 5/05 plantings however, the *r* was negative and not significant. Across planting dates *r* was low ($r=0.23$) and also of low significance ($P<0.05$). These data are in sharp contrast to those for GFR (Table 2.5), where all correlations were significant.

The analyses of variance for GFP for individual and across Waimanalo planting dates are shown in Tables 2.13 and 2.14, respectively. The variations among replications for GFP were not significant for all planting dates as observed also for GFR data (Tables 2.6, 2.7). For the individual ANOVA (Table 2.13), variations among inbreds were significant only during the 8/04 planting ($P<0.05$). There were no significant differences between GFP among inbreds during the 3/05 and 5/05 plantings. Grain filling periods among hybrids were significant in all planting dates. Heterosis (inbreds versus hybrids) was not significant during the 8/04 planting month, but was observed to be significant during the 3/05 ($P<0.01$) and 5/05 ($P<0.01$) plantings.

For the combined ANOVA of GFP (Table 2.14), planting dates provided forty times the mean square of entries and were highly significant ($P<0.01$). The replication within planting dates was not significant, consistent with the ANOVA for the individual planting dates. Significant differences were found among inbreds ($P<0.01$) and hybrids ($P<0.05$) and heterosis ($P<0.01$). The inbreds x M interaction was not significant which indicates that inbred GFPs were consistent among planting dates. The hybrids showed significant interactions with the month for GFP ($P<0.05$). Compared to GFR, the

Table 2.13. Mean squares for grain filling period within individual Waimanalo planting dates.

Source	df	Planting dates		
		8/04	3/05	5/05
Entries	35	25.40 *	19.92 **	17.36 **
Inbreds	7	34.90 *	15.41 ns	6.21 ns
Hybrids	27	23.38 *	12.86 *	18.18 **
I vs H	1	13.37 ns	241.97 **	73.24 **
Reps	1	6.74 ns	0.79 ns	0.04 ns
Error	35	12.67	6.75	7.48
Total	71			
CV%		13.1%	7.9%	7.7%
Grand mean		27.12	32.73	35.75

Table 2.14. ANOVA for GFP across Waimanalo planting dates.

Source	df	SS	MS	F	F0.05	F0.01
Months	2	2,761.54	1,380.77	546.79 **	3.09	4.82
Reps in Months	4	7.58	2.53	0.28 ns	2.69	3.98
Entries	35	1,206.52	34.47	2.44 **	1.54	1.84
Inbreds	7	282.60	40.37	5.00 **	2.10	2.82
Hybrids	27	666.86	24.70	1.66 *	1.60	1.93
I vs H	1	257.06	257.06	7.19 **	3.93	6.89
Entry x Month	70	987.16	14.10	1.56 *	1.43	1.66
Inbreds x M	14	113.02	8.07	0.90 ns	1.79	2.26
Hybrids x M	54	802.61	14.86	1.65 *	1.46	1.71
(I vs H) x M	2	71.52	35.76	3.97 *	3.09	4.82
Pooled Error	102	919.27	9.01			
Total	212	5,882.06				

Mean	31.865
CV %	9.42%
$LSD_{0.05}$ Inbreds	7.68
$LSD_{0.05}$ Hybrids	6.44

interaction among inbreds with the month for GFP was not significant. Heterosis was also observed not to be consistent across months ($P<0.05$).

2.3.2.2 Diallel analysis of grain filling period

For the analyses across the three planting dates, Hi57 was had the highest GCA for filling period (1.21), followed by Hi65 (0.50) and Hi62 (0.46) (Table 2.15). The lowest combining inbreds (shortest periods) were Hi60 (-0.94), Hi67 (-0.86) and Hi26 (-0.47). For the analysis of specific combining ability effects, the highest SCA hybrid was observed to be Hi60 x Hi26 (3.34). This was followed by Hi62 x Hi65 (1.86), Hi53 x Hi62 (1.56), Hi60 x Hi61 (1.24), and Hi60 x Hi62 (1.21). Three of these involved Philippine inbred Hi62 as one of the parents. Hybrids that were identified to have the least SCA effects (i.e., shorter grain fill) were Hi53 x Hi60 (-1.97), Hi60 x Hi65 (-1.88), and Hi57 x Hi60 (-1.44), all of which had the temperate parent Hi60 (Mo17) as one parent.

General and specific combining ability effects for grain filling periods were determined for individual and combined planting dates. For the trial planted on 8/04, highest GCA effects for GFP were obtained by Hi57 (3.80), followed by Hi65 (0.60) and Hi53 (0.38) (Table 2.15, bold face below diagonal). Among inbreds that included low GCA effects were Hi26 (-1.89), Hi61 (-1.44), Hi60 (-0.57), Hi67 (-0.52) and Hi62 (-0.36). For the analysis of SCA effects, hybrid Hi53 x Hi60 had the lowest SCA (-6.20) while Hi60 x Hi26 had the highest (8.52). Four inbreds crossed to Hi26 resulted to

Table 2.15. GCA (below diagonal) and SCA effects for GFP within individual and across Waimanalo planting dates.

(a) - Combined

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**0.36**	0.71	-1.97	1.02	1.56	1.09	1.16	0.69
Hi57		**1.21**	-1.44	0.54	0.91	0.40	-1.13	-0.35
Hi60			**-0.94**	1.24	1.21	-1.88	-0.45	3.34
Hi61				**-0.25**	0.27	0.11	-0.68	0.04
Hi62					**0.46**	1.86	0.46	0.73
Hi65						**0.50**	0.67	1.30
Hi67							**-0.86**	0.81
Hi26								**-0.47**

(b) - 8/04

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**0.38**	1.31	-6.20	-0.62	1.13	0.89	2.13	2.00
Hi57		**3.80**	-0.87	3.02	2.54	0.76	-3.98	-2.17
Hi60			**-0.57**	1.65	0.55	-3.51	-0.18	8.52
Hi61				**-1.44**	-2.78	-2.16	-0.72	-0.55
Hi62					**-0.36**	0.70	2.07	0.77
Hi65						**0.60**	3.70	-0.56
Hi67							**-0.52**	-0.98
Hi26								**-1.89**

(c) - 3/05

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**1.26**	-0.09	1.38	2.88	2.66	5.43	0.25	-0.60
Hi57		**0.74**	-3.27	0.89	0.37	0.87	-2.25	0.65
Hi60			**-1.20**	2.68	3.04	-1.10	-1.67	4.94
Hi61				**0.32**	1.10	0.10	0.87	0.21
Hi62					**0.52**	1.69	0.63	-0.28
Hi65						**-0.0013**	-0.54	4.08
Hi67							**-1.52**	2.50
Hi26								**-0.11**

(d) - 5/05

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**-0.22**	1.64	-3.05	1.81	2.46	-1.97	2.26	1.36
Hi57		**0.28**	-1.61	-1.74	0.72	-0.02	1.69	0.13
Hi60			**-1.97**	0.61	1.24	-2.89	0.05	-0.08
Hi61				**0.11**	2.78	2.53	-2.85	0.51
Hi62					**1.69**	5.04	-0.88	2.44
Hi65						**1.40**	-0.49	1.68
Hi67							**-1.40**	1.73
Hi26								**0.11**

negative SCA effects. Higher SCA hybrids that followed Hi60 x Hi26 were Hi65 x Hi67 (3.70), Hi57 x Hi67 (3.02), Hi57 x Hi62 (2.54) and Hi53 x Hi67 (2.13).

General combining ability effects was highest for Hi53 (1.26) for the trial planted in 3/05 (Table 2.15). This was followed by Hi57 (0.74) and Hi62 (0.52). Lowest GCA effects for GFP was obtained by Hi67 (-1.52), followed by Hi60 (-1.20). For the analysis of SCA effects for this month, Hi53 x Hi65 had the highest SCA (5.43) which was followed by Hi60 x Hi26, Hi65 x Hi26, Hi60 x Hi62, and Hi53 x Hi61 which were noted to have SCA effects of 4.94, 4.08, 3.04 and 2.88, respectively.

For the trial planted on 3/05, GCA effects ranged from -1.97 (Hi60) to 1.69 (Hi62) (Table 2.15). Higher combining inbreds for GFP followed Hi62 include Hi65 (1.40), Hi57 (0.28), Hi61 and Hi26, both of which had GCA effects of 0.11. Specific combining ability effects were highest for Hi62 x Hi65 (5.04), followed by Hi61 x Hi62 (2.78), Hi53 x Hi62 (2.46) and Hi62 x Hi26 (2.44). Three inbreds crossed to Hi65 resulted in negative SCA values. These were Hi53, Hi57 and Hi60, with SCA effects of -1.97, -0.02, and -2.89, respectively. Hybrids that had negative SCA effects include Hi53 x Hi60 (-3.05), Hi60 x Hi65 (-2.89) and Hi61 x Hi67 (-2.85).

General combining abilities of inbreds varied across the three planting dates (Figure 2.6). Inbred Hi57 increased GFP (GCA > 0.00) under low PAR and temperature (8/04), and reduced GFP under high PAR and temperature in 3/05 and 5/05 (GCA < 0.00). Inbred Hi61 reduced GFP in 8/04 and increased GFP in 3/05 and 5/05. Despite reduced GFP in 8/04, Hi61 increased GFR in 8/04 (Figure 2.5) under low PAR and temperature to compensate for dry matter accumulation in the grain. Inbred Hi60 reduced

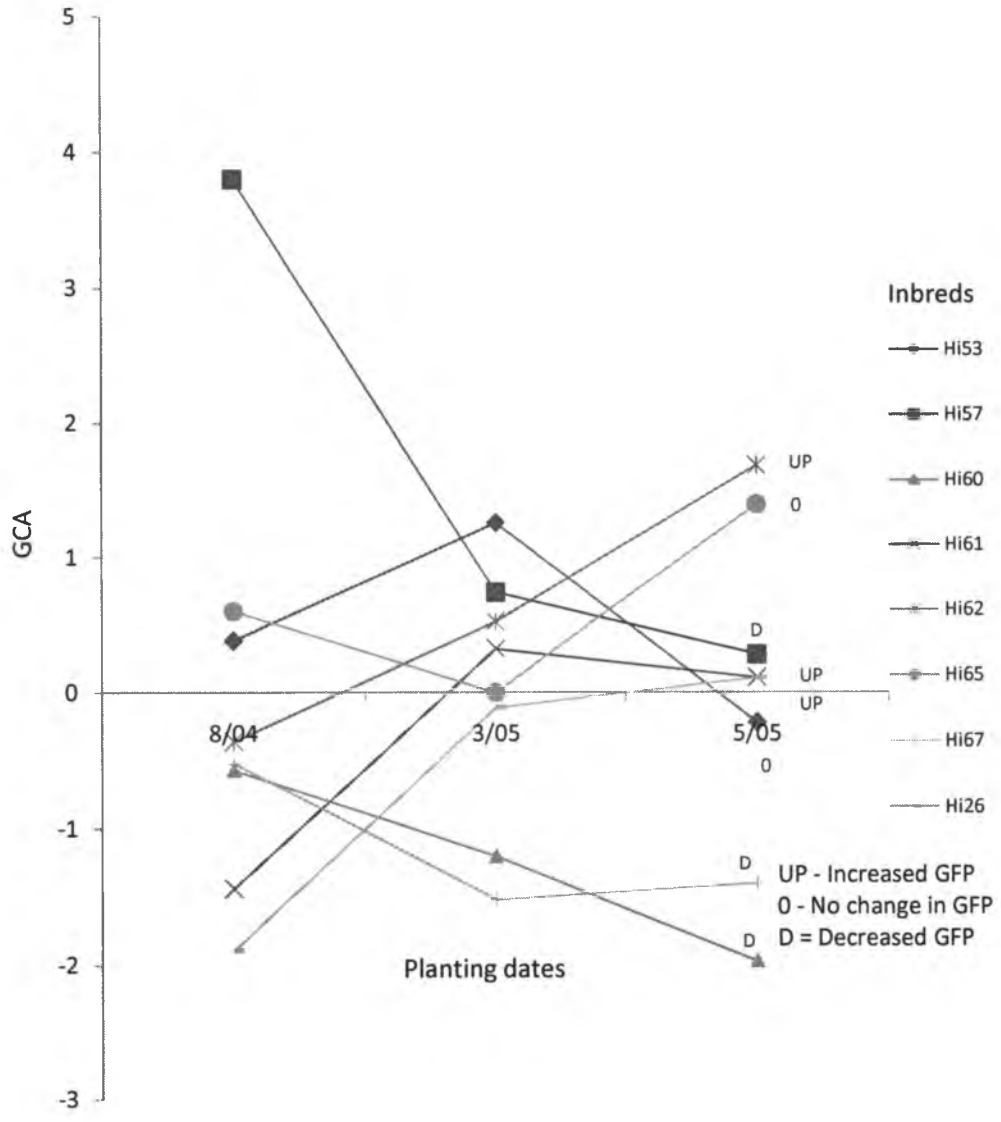

Figure 2.6. General combining ability x month interaction for GFP.

GFP (GCA <0.00) under higher PAR and temperature (3/05 and 5/05) (Figure 2.6). This inbred was originally bred to mature early to avoid frost damage (temperate short month). Hence under high PAR, Hi60 appears to reduce GFP but also increase GFR (Figure 2.5) to compensate for dry matter accumulation.

Analysis of variance showed that both GCA and SCA effects were important in the genetic control of GFP ($P<0.01$) (Table 2.16). For the trials planted on 8/04 and 5/05, the ratios of GCA to SCA effects were 2.64 and 1.57, respectively, indicating the predominance of GCA over SCA effects. For the trial planted on 3/05 the ratio was 0.63, suggesting that SCA effects were more important than GCA effects.

General combining ability ($P<0.01$) were the most significant in the genetic control of GFP in the combined analysis of variance (Table 2.17). The ratio of GCA to SCA mean squares for GFP was 2.15. Interactions of GCA and SCA with months were significant ($P<0.01$) for GFP, as they have been for GFR.

Table 2.16. Analysis of variance for combinining ability for GFP within individual Waimanalo planting dates.

Source	df	Planting dates		
		8/04	3/05	5/05
GCA	7	30.48 **	8.95 **	15.42 **
SCA	20	11.56 **	14.30 **	9.79 **
Error	35	2.11	2.11	2.31
Ratio				
2GCA/(2GCA+SCA)		0.84	0.56	0.76
GCA:SCA		2.64	0.63	1.57

Table 2.17. Analysis of variance for combining ability effects for GFP across Waimanalo planting dates.

Source	df	SS	MS	Fc	F0.05	F0.01
GCA	7	157.94	22.56	1.398 ns	2.764	4.278
SCA	28	294.51	10.52	1.408 **	1.678	2.078
GCA x M	14	226.03	16.14	3.583 **	1.790	2.262
SCA x M	56	418.36	7.47	1.658 **	1.458	1.703
Error	102	459.63	4.51			

Ratio	
2GCA/(2GCA+SCA)	0.75
GCA:SCA	2.15

2.4 Discussions

2.4.1 Grain filling rate

The inbred materials used in this study represent different heterotic groupings originating from different geographical locations. In Hawaii, these inbreds were selected during several generations of inbreeding and backcrossing to incorporate resistance to maize mosaic virus, rusts, blights and other diseases (Brewbaker, 1997, Brewbaker and Josue, 2007).

Grain filling rates were highest for Hi61, derived from Zimbabwe's N3 (SR52F), and for Hi53, derived from Colombia inbred ICA L210 (Cuban Flint-5832#). In a previous study by Fahrner (1991), Hi53 was also among inbreds with high rates of grain fill (10.39 g day^{-1}) at Waimanalo during the summer (May – August). In the present study, slow filling inbreds were Hi60 and Hi65. Inbred Hi60 was derived from temperate Mo17 (=CI187-2 x C103), while Hi65 was bred from Tx601 (Yellow Tuxpan).

Inbred performances for GFR were highly correlated with their corresponding hybrid array means. Highest hybrid array means were observed for Hi61 and Hi53. Mid-parent heterosis in all hybrids was positive for GFR. Variations among planting dates were also highly significant for GFR related to large seasonal differences in light and temperature across the Waimanalo growing planting dates. Variation between replications for GFR was very low and non-significant, a reflection of the homogeneity of experimental soils in Waimanalo that had been planted continuously to corn since the 1960s.

Variation in GFR was greatly influenced by seasonal differences, as revealed by significant genotype x month interactions. In contrast to the strong genotype x month interaction effects for GFR in this study, Cross (1975) did not find any significant differences for the hybrids x years interaction for GFR in maize diallel trials planted in two different years at one location in Fargo, North Dakota. Similarly, Katsantonis et al. (1986) did not find significant differences in the hybrids x years interaction also for GFR in maize diallel trials planted in two different years in Thessaloniki, Greece. Ottaviano and Camussi (1981) reported non-significant hybrid by month interactions for GFR among diallel hybrids grown in Milano and Pavia, Italy. All of these studies were in temperate regions where yields vary minimally from year to year compared to Waimanalo, where yields double from month to month (Jong et al., 1982).

Variations between inbreds and hybrids were significant for GFR. Fahrner (1991) also reported highly significant heterosis effects for GFR and GFP for trials planted at Waimanalo and Kapaa. For the current study, GFR heterosis was inconsistent across planting dates as revealed by inbreds versus hybrids x M interactions. Mid-parent heterosis for GFR was positive in all hybrids. The magnitude of heterosis for allogamous or cross-pollinating crops such as maize is greater than autogamous or self-pollinating crops such as wheat and rice.

General combining ability (GCA) and specific combining ability (SCA) effects were determined for GFR in three Waimanalo planting dates. Information on the genetic control was based on GCA and SCA mean squares, measures of additive and non-additive gene effects, respectively. Based on the magnitudes of GCA effects, inbreds

Hi53 and Hi61 consistently increased GFR, despite temperature and PAR differences among the three planting dates. Inbred Hi60 (Mo17) reduced GFR under low PAR and temperature and increased GFR under high PAR and temperature. Katsantonis et al. (1986) in Thessaloniki, Greece reported Mo17 to have the highest GCA for GFR based on a diallel of 6 inbred lines. Similarly, Ottaviano and Camussi, (1981) in Italy also reported Mo17 to have the highest GCA for GFR (1981) based on a diallel of 10 inbreds. Both studies were under long-day temperate conditions with PAR values expected to be 50% greater than possible in Hawaii.

High ratios of GCA to SCA mean squares were observed for GFR indicating that genetic control is largely due to the additive type of gene action. At Waimanalo, the ratio of GCA to SCA mean squares for GFR was 4.83 for the combined analysis. The predominance of GCA effects corroborated the findings of previous studies involving non-tropical maize germplasm. Greater mean square ratios of GCA to SCA for grain filling rate were reported by Cross (1975) in a diallel of 7 maize inbred lines in Fargo, North Dakota (GCA:SCA = 14) and Katsantonis et al. (1986) in Thessaloniki, Greece (GCA:SCA = 7.98) from a diallel of 6 maize inbreds. Ottaviano and Camussi (1981) in Italy also obtained greater mean squares for GCA than SCA for grain filling rate (GCA: SCA = 10.73). Wang et al. (1999) in Baton Rouge, Louisiana, also reported greater GCA mean squares than SCA in male and female inbreds based on a Design II 4x4 mating scheme. The ratios of GCA to SCA effects for GFR in the present study were typically greater than that ratio of GCA to SCA mean squares for GFP, also as noted in the temperate studies. In contrast to the findings of this study and the previous reports,

Fahrner (1991) reported that SCA effects were more important than GCA effects (GCA:SCA = 0.45) in the genetic control of GFR and from diallel trials she planted at Waimanalo and Kapaa. The coefficients of variation in these trials however were very high and thus are not considered very reliable estimates.

Highly significant GCA x month and SCA x month interactions for GFR were also observed. Similar to this study, Ottaviano and Camussi (1981) reported a highly significant GCA x month interaction for GFR based on diallel trials planted in three planting dates, two years in Milano and one year in Pavia, Italy. In contrast, Cross (1975) in Fargo, North Dakota, and Katsantonis et al., (1986) in Thessaloniki, Greece, did not find any significant differences for years x GCA and years x SCA interactions for grain filling rate. In Waimanalo the differences in PAR and temperature between the autumn planting in 8/4 and the 2005 trials (Chapter 5) truly accounted for the significance of GCA and SCA x month interactions in this study.

With the prevalence of additive gene effects for GFR, this trait can be improved with breeding methods such as those used in population improvement that take advantage of additive variation. Hybrid breeding methods could also be used considering the significant SCA effects for GFR. However, the highly significant genotype x month interactions for GFR in Hawaii mandates breeding and evaluation in multiple planting dates through the year. This has been traditionally practiced in Hawaii (Brewbaker 2003).

2.4.2 Grain filling period

The inbred with the longest GFP was Hi57 (Ku1409, from Suwan 1(S) (C4) and the inbred with the shortest GFP was Hi62 (Pi17, Tropical x Temperate). Among the long duration inbreds cited from the work of Fahrner (1991) were Ki3=Ku1403 (52.6 days, Waimanalo - summer), and Ki14=Ku1414 (55.5 days, Kapaa - winter). Both are relatives of Hi57 and were also derived from the Suwan synthetic. Mid-parent heterosis for GFP in some hybrids was negative, which indicate that the mean GFP among the F1s were less than the mean GFP of the inbreds, suggesting heterosis for a reduction in the grain filling period. Negative heterosis for GFP was especially noted for crosses between tropical inbreds and Hi60, a Mo17 conversion originally from a temperate background. Largest heterosis for reduction in GFP was observed for Hi57 x Hi60.

Inbred performances for GFP were also highly correlated with hybrid array means. Month effects were also highly significant for GFP. A very low and non-significant variation occurred among replications for GFP, is a reflection of the homogeneity of soils in Waimanalo.

Grain filling periods varied among the 8 inbreds and their 28 F1 diallel hybrids within individual and across Waimanalo planting dates. Strong genotype x month interaction effects were also observed for GFP, suggesting inconsistency across the three planting dates. This corroborates the finding of Katsantonis et al. (1986) in Thessaloniki, Greece, who reported that hybrids x years interaction for GFP was significant based on diallel trials. In contrast to the significant genotype x month effects obtained from this study at Waimanalo, Cross (1975) did not find any significant differences for the hybrids

x years interaction for GFP in maize diallel trials planted in two different years at a same site in Fargo, North Dakota. Ottaviano and Camussi (1981) in Italy also reported non-significant hybrid by month interactions for the effective filling period duration among diallel hybrids grown at Milano and Pavia, Italy. At Waimanalo, the differences in PAR and temperature between the 8/04 and 2005 trials were indeed quite large (Chapter 5) thus resulting in as a strong genotype x month interaction for GFP as it was for GFR. In the studies of Cross (1975) and of Ottaviano and Camussi (1981), the long durations of light (>16 hours) during the summer were identical year after year thus resulting to no significant hybrid x years interactions.

Variations among heterosis effects were significant also for GFP. Fahrner (1991) also reported highly significant GFP heterosis effects. Heterosis was inconsistent across planting dates for GFP as revealed by greater mean squares and the significance of the inbreds versus hybrids x month interactions.

General combining ability and specific combining ability effects were determined also for GFP. Based on the magnitudes of GCA effects, inbred Hi57 increased GFP in the winter trials and reduced GFP in the summer. Inbred Hi60 reduced GFP during the winter and increased GFP in the summer trials. In the study of Katsantonis et al. (1986) in Thessaloniki, Greece, Mo17 also had the highest GCA for GFP. In contrast, Ottaviano and Camussi (1981) based on the two locations in Italy reported Mo17 to have the lowest GCA for effective filling period duration.

Larger GCA effects as opposed to SCA effects were also observed for GFP within individual and across Waimanalo planting dates indicating the genetic control is largely

due to the additive type of gene action. At Waimanalo, the ratio of GCA to SCA mean squares for GFP was 2.15. The predominance of GCA effects for GFP agreed with the findings of previous studies. Higher mean square ratios of GCA to SCA for GFP (GCA:SCA = 8.88) were obtained by Cross (1975) in a diallel of 7 maize inbred lines in North Dakota. In Thessaloniki Greece, Katsantonis et al. (1986) found this ratio to be 1.5 from a diallel of 6 maize inbreds. The prevalence of GCA effects for GFP were also reported in Italy (GCA: SCA = 5.34) by Ottaviano and Camussi, (1981) and in Baton Rouge, Louisiana by Wang et al. (1999) among male and female inbreds based on a Design II 4x4 mating scheme. Similar to the aforementioned studies, the ratios of GCA to SCA effects for GFP were typically lesser than GFR. In contrast to the predominance of additive genes effects for GFP in this study and the aforementioned reports, Fahrner (1991) found that SCA effects were more important than GCA for GFP from diallel trials planted at Waimanalo and Kapaa. This study however had large coefficients of variation for GFP and therefore estimates of combining ability effects may not be reliable.

Significant GCA x month and SCA x month interactions for GFP were obtained in this study in Waimanalo. This corroborates the findings of Katsantonis et al. (1986) who also found significant differences in the years x GCA and years x SCA for GFP. Ottaviano and Camussi (1981) also reported a significant GCA x season interaction for GFP. In North Dakota, Cross (1975) did not find any significant differences in years x GCA and years x SCA interactions.

With the prevalence of additive gene effects for GFP, this trait can be improved with breeding methods that take advantage of additive variation. Hybrid breeding

approaches with evaluation in multiple planting dates could also be used considering the significant SCA effects for GFP. The inconsistency of GFP across planting dates as reflected in the significant genotype x month interactions requires breeding for improved GFP in multiple planting dates, months or environments.

CHAPTER 3
GENERATION MEAN ANALYSIS OF GRAIN FILLING RATE AND PERIOD IN MAIZE

3.1 Introduction

Previous studies (Cross, 1975; Katsantonis et al., 1986; Wang et al., 1999) including the diallel study conducted in the three Waimanalo planting dates have shown that grain filling rate and grain filling period in maize are controlled by additive and non-additive gene effects, with the additive gene effects in greater magnitude. On the basis of the above findings, generation mean analysis was conducted to partition and estimate non-additive genetic effects for grain filling rate and grain filling period in maize.

Information on the types of allelic and non-allelic interactions would influence the appropriate breeding methods for the improvement of grain filling rate and grain filling duration. In wheat (*Triticum aestivum*), Mashiringwani et al. (1994) reported that grain filling rates were controlled by additive, dominance and additive x additive gene effects.

This study was conducted to estimate the magnitude of additive, dominance, and non-allelic gene effects namely; additive x additive, additive x dominance, and dominance x dominance gene effects for grain filling rate and grain filling period in maize using generation mean analysis in two Waimanalo planting dates. For this study, the non-allelic gene effects were estimated using the model described by Hayman (1958) and confirmed using joint scaling tests with weighted regression analysis (Rowe and Alexander, 1980).

3.2 Materials and Methods

3.2.1 Maize inbred lines

Generation mean analysis (GMA) was performed to estimate allelic and non-allelic gene interactions controlling grain filling rate (GFR) and grain filling period (GFP). Six populations were used for GMA analysis - P1, P2, F1, F2, and the backcrosses BCP1 and BCP2. Data from the diallel trial of 8/04, under conditions of cool climate with low solar radiation, were used to choose parents for the two GMA populations. Hi60 was selected to represent slow GFR group (5.71 mg $k^{-1}day^{-1}$) while Hi53 was selected to represent fast GFR group (10.08 mg $k^{-1}day^{-1}$). For GFP, Hi57 was selected to represent the long period (34.4 days) and Hi62 the short period (23.9 days). The two sets of populations were generated in February 2005 and planted in two different Waimanalo planting dates. GFR trials were planted June 8, 2005 (6/05) and February 2, 2006 (2/06). GFP trials were planted July 25, 2005 (7/05) and April 12, 2006 (4/06). Each trial was a randomized complete block with three replications. The parents were randomized separately from the other entries to prevent competition and shading. Plot size was 2 rows ($7.5m^2$) each for P1 and P2, 3 rows ($11.25\ m^2$) each for BCP1 and BCP2, 2 rows ($7.5m^2$) of F1 and 5 rows ($18.75m^2$) of the F2. Fertilizer application and weed management were conducted in the same manner described previously for the diallel trials (Chapter 2).

3.2.2 Measurement of grain filling rate and period

Grain filling rates and grain filling periods were determined in the same manner described previously for the diallel trials except that the sampling of kernels was done on a per plant basis for the backcross and the F2 populations. For these populations, a total of 10 kernels were sampled at the middle of the primary ear. In the middle of each ear, the husks were partially cut and folded to expose the kernels and tied with rubber bands after sampling. Kernels were sampled at 14, 21, 28, 35 days after silk emergence and one final harvest at physiological maturity. The number of days from planting to silk emergence was determined when the silks had emerged about 1-2 inches. A total of 15 plants from each backcross population, and 30 plants from the F2 population were randomly selected in the inner rows of each plot in each replication. Five ears per plot were sampled for the parents and F1's and processed according to the procedure described previously for the diallel trials. Kernels sampled from individual plants were placed in shoot bags (Lawson™ 217) and kept frozen at -10°C until all of the samples were collected. When all samples were collected, the samples oven dried at 70°C for 7 days and weighed.

3.2.3 Analysis of variance for generations

Analyses of variance for individual and combined planting dates were conducted for each generation prior to generation mean analysis in spreadsheet (Brewbaker 2004). Table 3.1 shows the format of the ANOVA for the generations and the expectation of mean squares for the combined analysis.

Table 3.1. Format of the analysis of variance and the expected mean squares.

Source	df	EMS
Season (S)	1	$\sigma^2_e + r\sigma^2 r_{Sg} + rS\,\theta_g$
Rep (Planting dates) (r/S)	4	$\sigma^2_e + g\sigma^2 r_{Sg} + rS\,\theta_g$
Generations (g)	5	$\sigma^2_e + r\sigma^2_{Sg} + rS\,\theta_g$
Generation x S	5	$\sigma^2_e + r\sigma^2_{Sg}$
Pooled error	20	σ^2_e
Total	35	

The model used for the analysis of variance for generations is as follows.

$$Y_{ijkl} = \mu + \alpha_l + \beta_{k(l)} + \tau_i + (\alpha\,\tau)_{il} + \varepsilon_{ijkl}$$

Where; μ = grand mean
α_l = season effect
$\beta_{k(l)}$ = reps within seasons effect
τ_i = generation effects
$(\alpha\,\tau)_{il}$ = generation by season interaction
ε_{ijkl} = experimental error

3.2.4 Generation mean analysis

Individual scaling tests were first performed for the GMA data for individual and combined planting dates. This analysis is often called the "three-parameter model" or "additive-dominance" model and assumes that the variation among generation means is due to additive and dominance gene effects without linkage or epistasis. The formulas for the computation of scaling tests are presented below (Hayman and Mather, 1955; Mather, 1949):

$$A = 2\overline{B}_1 - \overline{P}_1 - \overline{F}_1 \qquad V_A = 4V\overline{B}_1 + V\overline{P}_1 + V\overline{F}_1$$

$$B = 2\overline{B}_2 - \overline{P}_2 - \overline{F}_1 \qquad V_B = 4\,V\overline{B}_2 + V\overline{P}_2 + V\overline{F}_1$$

$$C = 4\overline{F}_2 - 2\overline{F}_1 - \overline{P}_1 - \overline{P}_2 \qquad V_C = 16V\overline{F}_2 + 4V\overline{F}_1 + V\overline{P}_1 + V\overline{P}_2$$

The standard errors were calculated by taking the square root of the variances from each test and the significance of each scale was assessed using a t-test with the degrees of freedom equal to the sum of the number of individuals in each generation minus the number of replications. Joint scaling tests for the three parameter, model using weighted regression analyses of the generation means were also used to confirm these results and to estimate expected generation means and the genetic parameters m, a, and d (Rowe and Alexander, 1980). Computations of the matrices were done in Quattro Pro 10 (COREL Co. Ltd., 2001). Whenever the three parameter joint scaling test indicated presence of non-allelic interactions, additional parameters *i* (additive x additive), *j* (additive x dominance) and *l* (dominance x dominance) were included with the model, called the "six-parameter" model. The formulas for the estimation of the individual genetic parameters as described by Hayman (1958) are as follows:

Mean (m) = $\overline{F}_2$

Additive effect (a)= $\overline{B}_1 - \overline{B}_2$

Dominance effect (d) = $\overline{F}_1 - 4\overline{F}_2 - \frac{1}{2}\overline{P}_1 - \frac{1}{2}\overline{P}_2 + 2\overline{B}_1 + 2\overline{B}_2$

Additive x additive effect (aa) = $2\overline{B}_1 + 2\overline{B}_2 - 4\overline{F}_2$

Additive x dominance effect (ad) = $\overline{B}_1 - \frac{1}{2}\overline{P}_1 - \overline{B}_2 + \frac{1}{2}\overline{P}_2$

Dominance x dominance effect (dd) = $\overline{P}_1 + \overline{P}_2 + 2\overline{F}_1 + 4\overline{F}_2 - 4\overline{B}_1 - 4\overline{B}_2$

Computation of standard errors and significance of the genetic effects followed procedures described previously for the individual scaling tests. Weighted regression

analysis (Rowe and Alexander, 1980) was also used to determine which type of non-allelic interaction best explained variations among the generation means.

3.3 Results

3.3.1 Grain filling rate

Mean grain filling rates for the six populations were determined for the trials planted in June 2005 (6/05), February 2006 (2/06) and for the combined data (Table 3.2). Means of the parents Hi60 (P_1) and Hi53 (P_2) were 9.86 and 9.59 mg $k^{-1}day^{-1}$ in the 6/05 trial, with Hi53 unexpectedly filling faster than Hi60 (by 0.27 mg $k^{-1}day^{-1}$). However, for the trial planted 2/06 and for combined data, the mean GFR of Hi60 was slower than Hi53 as expected. Hi60 filled at a rate of 7.22 mg $k^{-1}day^{-1}$ in the 2/06 trial, while Hi53 filled at a rate of 9.20 mg $k^{-1}day^{-1}$. For the combined data, mean GFRs for Hi60 and Hi53 were 8.54 and 9.41 mg $k^{-1}day^{-1}$, respectively.

Analysis of variance was performed for the six GMA populations in the two planting dates (Table 3.3). Differences among the two planting dates were highly significant ($P<0.01$), while variations among generations and among replicates within planting dates were not significant. The interaction of generation with season was marginally significant ($P<0.05$), suggesting that grain filling rates among the six populations were affected differentially in the two Waimanalo planting dates.

Individual scaling tests for GFR (Table 3.4) were performed for individual and combined planting dates, following Mather and Jinks (1980). Non-allelic interactions were not indicated for the 6/05 trial. However, for the 2/06 trial and for the combined data, the A test was significant, indicating that there were possible non-allelic interactions involved in the expression of GFR.

Table 3.2. Grain filling rate for two parents, Hi60 (P1) and Hi53 (P2), F1, F2 and backcross (BCP1 and BCP2) generations.

Generations	Planting dates		Combined
	6/05	2/06	
P1	9.86 ± 0.227	7.22 ± 0.380	8.54 ± 0.221
P2	9.59 ± 0.282	9.20 ± 0.296	9.41 ± 0.204
F1	10.86 ± 0.291	9.65 ± 0.340	10.26 ± 0.224
F2	9.90 ± 0.200	9.31 ± 0.224	9.62 ± 0.134
BCP1	10.63 ± 0.140	9.44 ± 0.334	10.05 ± 0.179
BCP2	9.84 ± 0.189	9.81 ± 0.169	9.84 ± 0.127

Table 3.3. Analysis of variance of the generations for grain filling rate.

Source	df	SS	MS	F	F0.05	F0.01
Seasons	1	9.050	9.050	287.057 **	7.709	21.198
Reps (Season)	4	0.126	0.032	0.087 ns	2.866	4.431
Gens	5	10.972	2.194	1.722 ns	5.050	10.967
Gen x Season	5	6.371	1.274	3.533 *	2.711	4.103
Error	20	7.214	0.361			
Total	35	33.732				
Mean	9.71					
CV%	6.19%					

Table 3.4. Individual scaling tests on grain filling rate from the Hi60 x Hi53 family.

Test	Planting dates				Combined	
	6/05		2/06			
A= 2B1-P1-F1	0.535 ±	0.464 ^{ns}	2.010 ±	0.840 *	1.314 ±	0.476 **
B= 2B2-P2-F1	-0.773 ±	0.554 ^{ns}	0.757 ±	0.564 ^{ns}	0.018 ±	0.395 ^{ns}
C= 4F2-2F1-P1-P2	-1.577 ±	1.052 ^{ns}	1.503 ±	1.223 ^{ns}	0.042 ±	0.762 ^{ns}
D= 2F2-B1-B2	-0.669 ±	0.463 ^{ns}	-0.632 ±	0.584 ^{ns}	-0.645 ±	0.347 ^{ns}

Joint scaling tests for the three parameter (m, a and d) additive-dominance model using weighted regression analysis (Rowe and Alexander, 1980) were then performed to confirm the scaling tests, estimate the genetic parameters, and test the goodness of fit for the models being applied (Table 3.5). Significant deviations between observed and expected means were observed in the 6/05 trial ($\chi^2 = 9.81$, $P<0.05$) and for the combined data ($\chi^2= 9.06$, $P<0.05$). This confirmed the possible involvement of non-allelic interactions and indicated that variations in GFR means could not be fully explained by an additive-dominance model.

The significance of the three epistatic interactions - aa, ad, dd - were then tested using the six parameter model (Hayman, 1958) and five parameter model based on weighted regression analysis (Table 3.6). Estimates of the additive, dominance and epistatic effects varied in magnitude within and across planting dates. Dominance effects were significant for both planting dates ($P<0.05$) and for the combined data ($P<0.01$). Among epistatic interactions, the additive x dominance effects were significant for the 6/05 trial ($P<0.05$) and for the combined data ($P<0.05$). Additive x additive and dominance x dominance epistasis were not significant within individual and combined planting dates. Dominance x dominance effects were negative for the combined planting dates.

The five genetic parameters using weighted least squares were also determined for GFR (Table 3.6). Additive and dominance effects were not significant. The additive x additive effects were omitted from the model for the 6/05 trial, since they were not significant in the six parameter model. However, additive x dominance epistasis was

Table 3.5. Joint scaling test of the additive dominance model for grain filling rate from the trials in 6/05, 2/06, and combined data.

Generation	Env	No. of plants	Variance of mean	m	[a]	[d]	Observed	Expected	Difference O - E
P1	6/05	15	0.051	1	1	0	9.859	10.020	-0.161
	2/06	15	0.144				7.223	7.606	-0.383
	Combined	30	0.049				8.541	8.806	-0.265
P2	6/05	15	0.079	1	-1	0	9.593	9.205	0.388
	2/06	14	0.088				9.204	9.330	-0.126
	Combined	29	0.042				9.405	9.311	0.094
F1	6/05	15	0.085	1	0	1	10.859	10.725	0.134
	2/06	15	0.116				9.651	10.124	-0.473
	Combined	30	0.050				10.255	10.413	-0.158
F2	6/05	83	0.040	1	0	1	9.898	10.169	-0.270
	2/06	86	0.050				9.308	9.296	0.012
	Combined	169	0.018				9.625	9.736	-0.111
BCP1	6/05	45	0.020	1	0.5	1	10.626	10.372	0.254
	2/06	42	0.111				9.443	8.865	0.578
	Combined	87	0.032				10.055	9.610	0.445
BCP2	6/05	45	0.036	1	-0.5	1	9.839	9.965	-0.126
	2/06	45	0.029				9.806	9.727	0.079
	Combined	90	0.016				9.839	9.862	-0.023

X^2 1 d.f.	
6/05	9.811 *
2/06	6.354 ns
Combined	9.063 *

Table 3.6. Estimation of genetic parameters using the six and five parameter models for grain filling rate.

Hayman (1958)		Planting dates		
Parameter		6/05	2/06	Combined
Mean	m	9.898 **	9.308 **	9.625 **
Additive effect	a	0.787 **	-0.364 ns	0.216 ns
Dominance effect	d	2.471 *	2.703 *	2.572 **
Add x Add	aa	1.338 ns	1.265 ns	1.290 ns
Add x Dom	ad	0.654 *	0.627 ns	0.648 *
Dom x Dom	dd	-1.100 ns	-4.033 ns	-2.622 ns
Weighted least square		Planting dates		
Parameter		6/05	2/06	Combined
Mean	m	9.726 **	-	8.973 **
Additive effect	a	0.133 ns		-0.432 ns
Dominance effect	d	0.370 ns		2.100 **
Add x Add	aa	-		-
Add x Dom	ad	1.459 **		1.126 *
Dom x Dom	dd	0.763 ns		-0.818 ns

significant ($P<0.01$), confirming observations from the six parameter model. Dominance x dominance effects was not significant, confirming the results of the six parameter model. Weighted regression analysis was not performed for the trial in February 2006, since the three parameter additive-dominance model was the best fit to explain the variation among the generation means. Dominance ($P<0.05$) and additive x dominance effects ($P<0.01$) were significant for the combined data by least square estimation, which agreed with the magnitudes of dominance and additive x dominance estimates of the six parameter model improving its precision.

Weighted least squares were used to calculate expected generation means for the three (3P) and five (5P) parameter models in Table 3.7. Estimation of the additional genetic parameters for epistasis was required for the 6/05 trial and for the combined data. Additional genetic parameters were not estimated for the 2/06 trial, since the differences between observed and expected means were not significant. Chi-square tests revealed little or no significant variation among expected and observed means.

3.3.2 Grain filling period

Means of the six populations from the Hi57 (long duration) x Hi62 (short duration) family from the individual and combined planting dates are presented in Table 3.8. Mean grain filling periods for the two planting dates 7/05 and 4/06 were 33.2 and 33.1 days for Hi57 and Hi62, respectively. Similar minor differences characterized the two inbreds for each of the two trials. F1 hybrids showed the longest GFP values (mean 36.0 days), and BC to the short duration parent (mean 35.23 days). Grain filling of Hi57

Table 3.7. Expected generation means of 3 and 5 parameter model by weighted least square for grain filling rate.

Generation	Observed			6/05- Expected		2/06 - Expected		Combined	
	6/05	2/06	Combined	3P	5P	3P	5P	3P	5P
P1	9.86	7.22	8.54	10.02	9.86	7.61	-	8.81	8.54
P2	9.59	9.20	9.41	9.21	9.59	9.33		9.31	9.41
F1	10.86	9.65	10.26	10.72	10.86	10.12		10.41	10.26
F2	9.90	9.31	9.63	10.17	10.10	9.30		9.74	9.82
BCP1	10.63	9.44	10.06	10.37	10.53	8.87		9.61	9.88
BCP2	9.84	9.81	9.84	9.96	9.67	9.73		9.86	9.75
χ^2				9.769 *	3.156 ^{ns}	6.354 ^{ns}		9.063 *	3.444 ^{ns}

Table 3.8. Grain filling periods for two parents, Hi57 (P1) and Hi62 (P2), F1, F2 and backcross (BCP1 and BCP2) generations.

Generations	Planting dates		Combined
	6/05	2/06	
P1	37.22 ± 0.401	29.19 ± 0.936	33.20 ± 0.509
P2	36.45 ± 0.767	30.52 ± 1.090	33.06 ± 0.682
F1	36.18 ± 0.481	35.88 ± 0.944	36.03 ± 0.530
F2	35.18 ± 0.200	32.91 ± 0.426	34.15 ± 0.235
BCP1	34.55 ± 0.282	33.08 ± 0.539	33.82 ± 0.306
BCP2	35.23 ± 0.369	33.93 ± 0.521	35.23 ± 0.289

may have been delayed slightly (mean 29.19) because of ear infections by smut (*Ustilago maydis*) that was prevalent in the 4/06 season. The failure of these inbreds to show the significant differences in GFP observed previously is evident in the very small variations in GFP among the six generations using data from the combined trials, ranging from 33.1 to 36.0 days.

Analysis of variance for the generation means was performed prior to the estimation of the genetic parameters for generation mean analysis (Table 3.9). While the variation among planting dates was significant ($P<0.05$), the variations among generations, replications within planting dates, and generation x season interactions were not significant for the combined data.

Individual scaling tests for the Hi57 x Hi62 families were performed to determine whether non-allelic interactions were involved in the genetic control of GFP (Table 3.10). While the magnitude of the scaling tests varied within and across planting dates, all tests revealed that non-allelic interactions were negligible.

Joint scaling tests were performed for individual and combined data, despite the evidence that epistatic effects were not significant (Table 3.11). Chi-square tests for departure of observed from expected generation means were significant the combined data ($\chi^2=8.401$, $P<0.05$) and for the 7/05 trial ($\chi^2=27.87$, $P<0.01$), but not for the 4/06 trial. This not only confirms the result of the individual scaling test in this season but also suggests that the three parameter additive dominance model was adequate to explain the limited variation observed among GFP generation means. Since χ^2 for the trial in July

Table 3.9. Analysis of variance of the generations for grain filling period.

Source	df	SS	MS	F	F0.05	F0.01
Seasons	1	86.934	86.934	7.864 *	7.709	21.198
Reps (Seasons)	4	44.219	11.055	0.928 ns	2.866	4.431
Gens	5	32.654	6.531	0.482 ns	5.050	10.967
Gen x Seasons	5	67.780	13.556	1.138 ns	2.711	4.103
Error	20	238.334	11.917			
Total	35	469.920				

Mean	34.18
CV%	10.10%

Table 3.10. Individual scaling tests on grain filling period from the Hi57 x Hi62 family.

Test	Planting dates		Combined
	7/05	4/06	
A= 2B1-P1-F1	-4.305 ± 0.843 ^{ns}	1.098 ± 1.711 ^{ns}	-1.586 ± 0.956 ^{ns}
B= 2B2-P2-F1	-2.165 ± 1.168 ^{ns}	1.461 ± 1.778 ^{ns}	1.373 ± 1.039 ^{ns}
C= 4F2-2F1-P1-P2	-5.322 ± 1.521 ^{ns}	0.158 ± 2.920 ^{ns}	-1.710 ± 1.653 ^{ns}
D= 2F2-B1-B2	0.574 ± 0.612 ^{ns}	-1.200 ± 1.134 ^{ns}	-0.748 ± 0.631 ^{ns}

Table 3.11. Joint scaling test of the additive dominance model for grain filling period from the trials in 7/05, 6/06 and combined data.

Generation	Env	No. of plants	Variance of mean	m	[a]	[d]	Observed	Expected	Difference O - E
P1	7/05	15	0.161	1	1	0	37.219	36.217	1.002
	6/06	15	0.875				29.189	29.298	-0.109
	Combined	30	0.259				33.204	32.495	0.709
P2	7/05	9	0.588	1	-1	0	36.450	35.891	3.255
	6/06	12	1.188				30.524	30.895	4.611
	Combined	21	0.465				33.064	33.807	-0.743
F1	7/05	15	0.232	1	0	1	36.180	34.518	1.662
	6/06	15	0.891				35.877	36.266	-0.389
	Combined	30	0.281				36.029	35.709	0.32
F2	7/05	89	0.040	1	0	0.5	35.177	35.286	-0.109
	6/06	89	0.181				32.906	33.181	-0.275
	Combined	178	0.055				34.154	34.430	-0.276
BCP1	7/05	44	0.079	1	0.5	0.5	34.547	35.368	-0.821
	6/06	43	0.291				33.082	32.782	0.300
	Combined	87	0.094				33.823	34.102	-0.279
BCP2	7/05	42	0.136	1	-0.5	0.5	35.233	35.204	0.029
	6/06	45	0.271				33.931	33.581	0.350
	Combined	87	0.084				35.233	34.758	0.475

χ^2 =1 d.f.

7/05	27.87 **
4/06	1.506 ns
Combined	8.401 *

2005 and the combined data were significant, additional genetic parameters for the three non-allelic interactions were added in the model.

The significance of the three epistatic interactions - aa, ad, dd - were then tested using the six parameter model (Hayman, 1958) and five parameter model based on weighted regression analysis (Table 3.12). Using the 6-parameter model, additive effects were all negative and not significant while dominance effects were significant for the 4/06 trial and for the combined data. Epistatic interactions were generally non-significant, excepting the dd interaction for the 7/05 trial. In this season, the dd effect (7.62) was the largest observed within and across planting dates. Estimation of the genetic parameters for the five parameter model (Table 3.12) was after omitting the aa and ad effects for the 4/06 and combined trials, since they were not statistically significant in the six parameter model. Additive and dominance effects were not significant for the 7/05 trial, while the dd interaction was again seen to be highly significant ($P<0.01$).

Weighted least squares were used to calculate expected generation means for the three (3P) and five (5P) parameter models in Table 3.13. Additional genetic parameters were not estimated for the 5P model in the 4/06 trial, since the differences between observed and expected means were not significant. Chi-square tests for the 5P models revealed little or no significant variation among expected and observed means for 7/05 trial ($\chi^2=2.85$) and the combined data ($\chi^2= 1.40$). It is recognized that these theoretical models are in fact deemed inappropriate when scaling tests indicate no significances (Table 3.10), and the resultant effects must be interpreted with caution. Clearly the parent

Table 3.12. Estimation of genetic parameters using the six and five parameter models for grain filling period.

Hayman (1958)		Planting dates		
Parameter		7/05	4/06	Combined
Mean	m	35.177 **	32.906 **	34.154 **
Additive effect	a	-0.685 ns	-0.849 ns	-1.409 ns
Dominance effect	d	-1.803 ns	8.421 **	4.391 **
Add x Add	aa	-1.148 ns	2.401 ns	1.497 ns
Add x Dom	ad	-1.070 ns	-0.181 ns	-1.480 ns
Dom x Dom	dd	7.618 **	-4.960 ns	-1.283 ns
Weighted least square		Planting dates		
Parameter		7/05	4/06	Combined
Mean	m	38.326 **	-	33.134 **
Additive effect	a	-0.113 ns		0.070 ns
Dominance effect	d	-10.691 ns		2.016 **
Add x Add	aa	-1.208 ns		-
Add x Dom	ad	-		-2.998 ns
Dom x Dom	dd	8.5448 **		0.8795 ns

Table 3.13. Expected generation means of 3 and 5 parameter model by weighted least square for grain filling period.

Generation	Observed			7/05- Expected		4/05 - Expected		Combined	
	7/05	4/05	Combined	3P	5P	3P	5P	3P	5P
P1	37.22	29.19	33.20	36.22	37.00	29.30	-	32.49	33.20
P2	36.45	35.51	33.06	35.89	37.23	30.90		33.81	33.06
F1	36.18	35.88	36.03	34.52	36.18	36.27		35.71	36.03
F2	35.18	32.91	34.15	35.29	35.12	33.18		34.43	34.36
BCP1	34.55	33.08	33.82	35.37	34.76	32.78		34.10	33.65
BCP2	35.23	33.93	35.23	35.20	34.87	33.58		34.76	35.08
χ^2				27.87 **	2.85 ns	1.51 ns		8.40 *	1.40 ns

inbreds chosen for the GMA of GFP, Hi57 and Hi62, did not differ significantly enough to permit accurate estimates of quantitative genetic effects.

3.4 Discussions

The effectiveness of GMA analyses rests in part on the genetic differences among the selected parents. The choice of parents for these GFR and GFP populations was based on inbred performance in a single diallel trial planted 8/04, a trial that was subjected to low incident light and temperature values in the autumn of 2004. Subsequent evaluations of these inbreds in GMA trials were made in summer plantings, with relatively high PAR and temperature values. The differences among parents were much less in these GMA trials. GFR values for 8/04 were 5.71 mg $k^{-1}day^{-1}$ for Hi60 and 10.08 for Hi53, but for combined GMA plantings they were 8.54 for Hi60 and 9.41 for Hi53. GFP values for 8/04 were 28.9 days for Hi62 and 34.4 for Hi57, but for combined GMA plantings they were 33.1 for Hi62 and 33.2 for Hi57. As noted in analyses of the diallels, this seasonal difference and its interactions with genotypes appears to be fundamental. It is possible that evaluations of the GMA populations under the cool, low-light conditions of Hawaii's winters would reveal much greater evidence of genetic effects.

The GMA analyses of GFR and GFP data revealed little convincing evidence of departure from a simple model of additive and dominance variance, without compelling interactions. In some instances, however, the ad interactions were significant for GFR and the dd interactions significant for GFP. Hybrid vigor in GFR and GFP was evident in both the F1 and F2 populations, and in backcross populations, and was evident in

significant dominance effects in the GMA analyses. This study allowed an estimation of the genetic effects that was mostly confounded with the interaction components and the season.

Selections of inbreds with consistent performance for GFR and GFP under specific planting dates are recommended for a future study. Inbreds that consistently increased grain filling rates (GCA > 0.00, Chapter 2) in the three Waimanalo planting dates were Hi53 and Hi61 while inbreds that reduced GFR were Hi65 and Hi67 (GCA < 0.00). Populations for GMA analysis out of Hi53 x Hi67 were made in February 2, 2006 and were evaluated in trials to determine non-allelic interactions for GFR. Inbreds that consistently increased GFP include Hi57 and Hi65 while inbreds that reduced GFP were Hi60 and Hi67.

The use of recombinant inbred lines (RILs) reduce the confounding effects of heterosis and allows the evaluation of fixed inbred genotypes across different planting dates. The SET G RIL population (Hi31 x Ki14) was reported previously by Moon et al. (1999) to be segregating for kernel weights. Kernel weights in this study were highly correlated with GFR (Chapter 4) and were the basis for choosing the SET G population to identify putative QTLs for GFR. In an initial study, an analysis of variance for 25 kernel weights (bulk of sibs from each inbred) were done for 100 of the SET G RILs and parents Ki14 and Hi31. Highly significant differences were found for RILs, parents and RILs versus parents. These RILs were also mapped previously for maize mosaic virus resistance by Ming et al. (1997) using restriction fragment length polymorphisms (RFLP).

A total of the original 102 RILs were seed increased in April 12, 2006. Problems with seed germination were encountered with the original Ki14 parents used as sub-lines. The RILs were planted in two Waimanalo planting dates, in May 3, 2006 (Summer) and August 14, 2006 (Fall) with two replications to study GFR and GFP. The inbreds Hi53, Hi60 and the new version of Ki14 were also included in the two trials. Ears were harvested in a manner described previously in Chapter 2 to determine GFR and GFP. Kernel weights for the two trials have yet to be determined to calculate GFR and GFP.

CHAPTER 4
CORRELATIONS OF AGRONOMIC TRAITS WITH GRAIN FILLING RATES AND GRAIN FILLING PERIODS

4.1 Introduction

The objective of this study was to determine how grain filling rate and grain filling periods relate to other agronomic traits in maize.

Correlation coefficients (r) were used to determine how grain filling rate and grain filling period relate to the following agronomic traits, (1) Days to mid-anthesis (DTA), (2) Days to mid-silk (DTS), (3) plant height (PH), (4) ear height (EH), (5) ear diameter (EL), (6) ear length (EL), (7) kernel row number (KRN), (8) kernel numbers (KN), (9) kernel weight (KW), (10) plant yield (YLD), (11) kernel density (KDEN), (12) Chlorophyll (SPAD) at 30 days after planting (DAP), (13) SPAD at 60 DAP, and (14) SPAD at 90 DAP described in Chapter 2. Correlation analyses were done for each of the three planting dates and the combined data. Coefficients of determination (r^2) were applied to describe the proportions of grain filling rates and grain filling periods explained by an agronomic trait.

Information on the relationships between grain filling rates or grain filling periods with other agronomic traits will guide in the selection procedures for the improvement of these traits. Grain filling rates in maize were reported previously to be significantly correlated with kernel weights (Fahrner, 1991; Wang et al., 1999). Maize grain yields were also reported to be correlated with grain filling periods (Cross, 1975; Daynard and Kannenberg, 1976).

4.2 Results

4.2.1 Grain filling rate

Relationships between GFR and other agronomic traits were determined using correlation coefficients (*r*). Kernel weights were highly and positively correlated with GFR in all the three planting dates and for combined data of both inbreds and their hybrids (Table 4.1). Kernel weights accounted for 77.44% ($P < 0.01$) of the total variation of inbred GFR. Magnitudes of *r* for inbred plant yield were inconsistent among the three planting dates. A correlation of -0.28 ($P<0.05$) was obtained for the combined analysis. Correlations between kernel densities were also inconsistent among the three planting dates. Most relationships of inbred GFR with agronomic traits were not significant. Days to mid-anthesis and mid-silk among inbreds were not significantly correlated with GFR. Plant height was positively correlated with GFR and consistent among the three planting dates. Ear diameters were negatively correlated with GFR, consistent for the 3/05 and 5/05 plantings and combined data. The correlation between ear length and GFR was significant in the 3/5 and 5/05 plantings but not in 8/04 (with low PAR and low temperature). Overall correlation between these two traits was only 0.18 ($P<0.05$). Kernel row numbers and kernel numbers were negatively correlated with GFR, the magnitudes of which were consistent among the three planting dates.

Correlations between chlorophyll concentration and GFR varied among the three growth stages and among planting dates. Magnitudes of correlation coefficients at 30 DAP among inbreds were consistent in all planting dates and for the combined analysis (Table 4.1a), the highest of which occurred in 8/04 under low PAR and temperature.

Table 4.1. Correlation coefficients between GFR and agronomic traits.

(a) Inbreds	Planting dates			
Traits	8/04	3/05	5/05	Combined
GFP	0.07	-0.35	-0.17 *	-0.15
DTA	0.04	0.05	-0.17 *	0.04
DTS	-0.22 *	-0.26 *	-0.29 *	-0.09
EH	0.67 *	0.16	0.01	-0.05
PH	0.45 *	0.49 *	0.49 *	0.35 *
ED	0.58 *	-0.56 *	-0.47 *	-0.35 *
EL	0.05	0.21 *	0.55 *	0.18 *
KRN	0.31 *	-0.80 *	-0.73 *	-0.59 *
KN	-0.13	-0.50 *	-0.02	-0.51 *
KW	0.70 *	0.89 **	0.96 **	0.88 **
YLD	0.52 *	-0.31 *	-0.04	-0.28 *
KDEN	0.29 *	0.52 *	-0.36 *	0.52 *
SPAD-30 DAP	0.61 *	0.50 *	0.18 *	0.44 *
SPAD-60 DAP	-0.72 *	-0.45 *	0.11	-0.27 *
SPAD-90 DAP	0.19 *	0.32 *	-0.03	0.43 *
(b) Hybrids	8/04	3/05	5/05	Combined
GFP	-0.20	-0.05	-0.50 **	-0.14 **
DTA	-0.22	-0.10	-0.57 **	-0.37 *
DTS	-0.30	-0.10	-0.57 **	-0.31
EH	0.21	-0.18	-0.69 **	-0.18
PH	-0.02	0.08	-0.30	-0.04
ED	0.38 *	-0.38 *	-0.63 **	-0.26
EL	0.11	0.35	0.72 **	0.40 *
KRN	0.06	-0.69 **	-0.68 **	-0.47 *
KN	-0.28	-0.04	0.12	-0.34
KW	0.81 **	0.77 **	0.73 **	0.86 **
YLD	0.56 **	-0.05	-0.11	0.06
KDEN	0.56 **	-0.07	-0.33	-0.23
SPAD-30 DAP	0.22	0.03	-0.09	0.13
SPAD-60 DAP	-0.32	0.002	0.37 *	-0.12
SPAD-90 DAP	0.11	0.18	0.40 *	0.02

However SPAD at 30 DAP accounted for only 19.36% of the total variation in GFR. Coefficients were not consistent for SPAD at 60 and 90 DAP among the three planting dates.

The relationships between GFR and the aforementioned traits were also determined for the hybrids (Table 4.1b). Correlation coefficients for kernel weight and GFR were exceptionally high for the hybrids and were positive and statistically significant among for the three planting dates and for the combined analysis. Kernel weights accounted for 73.96% of the total variation in GFR. Correlations between plant yield and GFR were inconsistent among planting dates. Kernel density was not significantly correlated with GFR. Days to mid-anthesis and mid-silk were negatively correlated with GFR among hybrids. Magnitudes of the coefficients were both negative for days to mid-anthesis and days to mid-silk in all three planting dates as they were for the inbreds. Kernel row numbers and kernel numbers were negatively correlated with GFR. Correlation coefficients for ear length and GFR were positive between the three planting dates. Compared to the trials in 8/04 and 3/05, ear length accounted for a larger variation in GFR in 5/05 which amounted to 51.84%.

Chlorophyll concentrations were not correlated with grain filling rates of hybrids. Unlike the inbreds that had positive and statistically significant coefficients at 30 DAP, the magnitudes of r were very low and inconsistent in all growth stages and the three planting dates.

4.2.2 Grain filling periods

Correlation coefficients between grain filling periods and the aforementioned agronomic traits varied greatly across the three Waimanalo planting dates among inbreds and hybrids (Table 4.2). In general, GFP increased in longer, later hybrids and inbreds. Days to mid-anthesis and days to mid-silking among inbreds were negatively correlated with GFP in all three planting dates and the combined analysis (Table 4.2a). Correlation coefficients between ear height and plant height with GFP were inconsistent among the three planting dates.

Correlations between ear diameter and GFP for inbreds were positive and significant among the three planting dates. Ear diameters accounted for 36.0% of the variation in GFP. Kernel row numbers and kernel numbers were also positively correlated with GFP but accounted for smaller variations in GFP only. Kernel weights were positively correlated with GFR in the autumn planting (8/04). Correlation coefficients however were not significant in 3/05 and 5/05.

Plant yields accounted for a large variation in GFP among inbreds. Correlations were 0.59 ($P<0.05$), 0.69 ($P<0.05$), 0.47 ($P<0.05$), respectively for the trials in 8/04, 3/05 and 5/05. In totality, plant yield accounted for 79.21% of the variation in GFP for inbreds. Correlations between kernel density and GFP were inconsistent among the three planting dates.

Chlorophyll concentrations in all the three growth stages were not associated with GFP among inbreds as they were for GFR (Table 4.2a). Magnitudes of r were low and inconsistent among growth stages and among planting dates.

Table 4.2. Correlation coefficients between GFP and agronomic traits.

(a) Inbreds	Planting dates			
Traits	8/04	3/05	5/05	Combined
DTA	-0.01	-0.27 *	-0.26 *	-0.21 *
DTS	-0.43 *	-0.16 *	-0.10	-0.42 *
EH	0.17 *	-0.11	0.37 *	0.29 *
PH	-0.22 *	-0.43 *	0.37 *	-0.20 *
ED	0.49 *	0.46 *	0.26 *	0.60 *
EL	0.08	0.24 *	-0.11	0.13
KRN	0.26 *	0.31 *	0.30 *	0.42 *
KN	0.21 *	0.26 *	0.16	0.47 *
KW	0.66 *	0.12	0.10	0.33 *
YLD	0.59 *	0.69 *	0.47 *	0.89 **
KDEN	0.32 *	-0.04	0.08	0.31 *
SPAD-30 DAP	0.06	0.07	-0.57 *	-0.13
SPAD-60 DAP	-0.16	0.27 *	0.05	-0.20 *
SPAD-90 DAP	-0.13	-0.28 *	0.30 *	-0.24 *

(b) Hybrids	8/04	3/05	5/05	Combined
DTA	0.22	-0.01	0.61 **	0.58 **
DTS	-0.002	0.13	0.72 **	0.50 **
EH	0.41 *	0.43 *	0.68 **	0.71 **
PH	0.05	0.43 *	0.62 **	0.40 *
ED	0.54 **	0.50 **	0.65 **	0.68 **
EL	-0.11	0.25	-0.55 **	-0.51 **
KRN	0.46 *	-0.02	0.18	0.28
KN	-0.26	0.20	-0.36	-0.33 *
KW	0.39 *	0.59 **	0.22	0.34
YLD	0.45 *	0.75 **	0.17	0.47 *
KDEN	0.10	-0.02	0.16	0.07
SPAD-30 DAP	-0.10	0.48 **	-0.10	0.13
SPAD-60 DAP	-0.35	-0.40 *	-0.41 *	-0.53 **
SPAD-90 DAP	0.05	-0.33	-0.27	-0.28

Correlation coefficients, for days to mid-anthesis and days to mid-silk were generally positive and significant among the hybrids (Table 4.2b). Ear heights and plant heights were positive and significantly correlated with GFP, consistent among the three planting dates and the combined data. Ear heights accounted for 49% of the total variation in GFP among hybrids. It was clear that late, tall hybrids consistently produced ears with longer grain-filling periods.

Ear diameters among hybrids were positively and significantly correlated with GFPs among the three planting dates and combined analysis (Table 4.2b). For the combined analysis, ear diameters explained 46.24% of the variation in GFPs. Correlation coefficients for kernel row number and kernel numbers were inconsistent and rarely significant among planting dates.

Positive correlations were observed between kernel weight and GFP among hybrids in the 8/04 and 3/05 plantings (Table 4.2b). Kernel weights accounted for a considerably large proportion in the variation in GFP in 3/05 which amounted to 34.81% ($P<0.01$). Plant yields were also positively and significantly correlated with GFPs. In 3/05 plant yield accounted for 56.25% ($P<0.01$) of the variation in GFP. Overall, plant yield accounted for 22.09% ($P<0.05$) of the variation in GFP across planting dates.

Kernel densities did not correlate well with GFP. The magnitudes of r were inconsistent among the three planting dates (Table 4.2b). Chlorophyll concentrations among the three growth stages for hybrids did not correlate well also with GFP. Correlation coefficients were inconsistent among the three planting dates (Table 4.2b).

4.3 Discussions

4.3.1 Grain filling rate

In this study, GFR was negatively correlated with GFP among the three planting dates and combined analysis. A negative correlation between GFP and GFR was reported by Cross in North Dakota (1975) (r= -0.15). This r value is comparable to the r values obtained for the combined data among inbreds (r = -0.15 ^{ns}) and hybrids (r= -0.14, P<0.01) grown in Waimanalo. Daynard and Kannenberg (1976) also obtained a negative correlation between dry matter accumulation rate and the effective filling period duration in Canada (r = -0.41) but could not verify this statistically because the variables were not measured independently. In contrast to the negative correlations obtained in this study, non-significant but positive correlations between GFR and GFP in maize were reported by Katsantonis et al. (1986), in Thessaloniki Greece (r= 0.43^{ns}), and Kang et al. (1986) using 10 Pioneer and 2 public maize hybrids (r= 0.46, P<0.01) grown at Columbia, Missouri. Similarly, Perenzin et al. (1980) obtained a positive correlation between GFR and GFP (r= 0.36 ^{ns}) in a study of 40 Italian maize open pollinated varieties.

Grain filling rate was significantly and positively correlated with kernel weight among inbreds and hybrids in this study. It was consistent among the three planting dates despite large differences in PAR and temperature between the autumn (8/04) and the summer (2005). In an earlier study by Fahrner (1991), significant and positive correlations between GFR and kernel weight were obtained among 96 maize inbreds planted in Waimanalo (r= 0.42, P<0.01) and at Kapaa (r= 0.23, P<0.05). Similarly, Wang et al. (1999) in Baton Rouge Louisiana reported a positive correlation between

kernel filling rate and kernel weight (r= 0.75, P<0.01). With the positive and high correlation between kernel weights and grain filling rates among the inbreds and hybrids, selection for higher kernel weights is predicted to increase grain filling rates.

For the combined analysis, plant yield among hybrids was not significantly correlated with GFR (r= 0.06^{ns}). This was similar to the findings of Cross (1975) who found no significant correlation between GFR and grain yield per se (r= -0.06 ^{ns}). Daynard et al. (1971) also reported that less than 16% of the yield differences among several maize hybrids grown in two different years could be explained by differences in their rates of dry matter accumulation.

Wang et al. (1999) proposed that higher grain filling rates may possibly affect sink-source relationships, which is the partitioning of nitrogen from the leaves to storage organs. This may eventually result in a reduction in chlorophyll leaf concentration. This was suggested by the negative association between SPAD and grain filling rate (-0.45), based on path coefficient analysis, genotypic (-0.24^{ns}) and phenotypic (-0.37^{ns}) correlation analysis. Grain filling rate was also negatively correlated with SPAD among inbreds (r = -0.27, P<0.05) and hybrids (r = -0.12^{ns}) for the combined analysis at 60 DAP at Waimanalo. Negative correlations were also observed in the 8/04 and 3/05 trials during the reproductive phase among inbreds. Sink-source relationships as proposed by Wang et al. (1999) cannot be verified here because of the very low and non-significant correlation coefficients between SPAD and GFR. In comparison to the negative correlation coefficients at 60 DAP, GFR was positively correlated with SPAD at 30 and 90 DAP for both inbreds and hybrids, but the correlation coefficients were however

significant only for inbreds. With the inconsistent and low correlation coefficients between GFR and chlorophyll concentration, SPAD may not be used as an effective selection index to improve GFR in maize.

4.3.2 Grain filling period

The significant and positive correlations between GFP and plant yield among inbreds (r = 0.89, P<0.01) and hybrids (r = 0.47, P<0.05) for the combined analysis in this study corroborate previous studies in maize. Daynard and Kannenberg (1976) reported a correlation of 0.44 (P<0.01) between grain yield and effective filling period duration. Cross (1975) found this correlation to be 0.81 (P<0.01). Daynard et al. (1971) in two different years found that 80% and 71% of the variation in grain yield in three maize hybrids could be explained by the differences in their effective filling period durations. Significant and positive correlations between these two traits were also reported by Katsantonis et al. (1986) in Thessaloniki, Greece (r =0.88, P<0.01) and Wang et al. (1999) (r =0.35, P<0.01). In Hawaii where climate conditions permit growing corn all year round, breeding focuses on selection for improved yield without regard to selection for short grain filling periods. In temperate regions with short growing seasons, breeding is focused on improved yield with short GFP hybrids, perhaps accounting for higher correlation coefficients between GFP and yield.

Chlorophyll concentration was not associated with GFP. With the low and inconsistent correlation coefficients between SPAD and GFP, SPAD may not be used as an effective selection index to improve GFP in tropical maize.

CHAPTER 5
EFFECTS OF LIGHT AND TEMPERATURE ON GRAIN FILLING RATE, GRAIN FILLING PERIOD AND OTHER AGRONOMIC TRAITS

5.1 Introduction

Temperature and photosynthetic active radiation (PAR) values were recorded in relation to grain filling rate, grain filling period, and agronomic traits in these trials. Primary emphasis was on the effects of light (PAR) and temperature on GFR and GFP values, but the studies were extended to include kernel weight, plant yield, kernel numbers and kernel row numbers.

Diallel trials were planted on July 7, 2004 (7/04) and August 30, 2004 (8/04) to represent summer and fall plantings, respectively. Additional trials were planted on March 16, 2005 (3/05) and May 15, 2005 (5/05) representing spring and summer conditions. The trial in 7/04 was subsequently excluded from the analysis because of the inadequate sampling of ears to determine GFR and GFP. Photosynthetic active radiation data was not available in 2004, therefore the mean PAR values in 2005 and 2006 were used to compare with the trial in 8/04. Measurements of PAR were made using a quantum light sensor (Spectrum Technologies, Plainfield IL). Since light and temperature are understood to be highly correlated and inseparable, multiple linear regression analysis was used to compare GFR and GFP values (y) with PAR (x_1) temperature (x_2). For the regression analysis, only the mean daily PAR and temperatures during the effective filling period duration (EFPD) for each season were used. These varied from approximately 14 days to 42 days after the date of 50% silking. Coefficients of determination were calculated for each individual inbred and hybrid using the data in

each replication across the three planting dates. Tests of significance for regression for both PAR (x_1) and temperature (x_2) were conducted using F-tests.

The PAR values varied greatly for the three trials (from 18.11 to 42.71 mol m^{-2} day^{-1}) while the correlated temperatures values differed only slightly (from 24.3 to 26.3°C). The following discussions will assess correlations of agronomic traits concurrently with PAR and temperature.

5.2 Results

5.2.1 Effects of PAR and temperature

5.2.1.1 Grain filling rate

Mean temperature among the three planting dates were slightly different as opposed to light values during the effective filling period duration (Table 5.1). The 8/04 trial was characterized by the least amount of PAR (18.1 moles m^{-2} day^{-1}) and temperature (24.3°C). Higher PAR values (42.7 moles m^{-2} day^{-1}) were recorded in the 3/05 trial while the highest mean temperature was recorded in the 5/05 trial (26.8°C).

Light and temperature significantly influenced grain filling rates among entries with light making the greatest contribution to the overall variation in grain filling rates. Mean grain filling rates were least for both inbreds and hybrids in the 8/04 planting (Table 5.2) characterized by low PAR and temperature, and were similar in 3/05 and 5/05 with similar levels of PAR and temperature (Table 5.1). Coefficients of determination varied greatly among the inbreds and hybrids which greatly improved when PAR and temperature were used to calculate the regression (Table 5.2). On average, variation among grain filling rates as explained by light and temperature was 54% among inbreds and 61% among hybrids. Rates of grain fill for inbreds Hi60 (r^2=0.70, P<0.05), a temperate dent conversion, and Hi61 (r^2 = 0.95, P<0.01) a highland dent were accounted largely by PAR (Table 5.2). Array means were highest for Hi61 and Hi62.

Light also accounted largely for rates of grain fill among hybrids. Hybrids Hi60 x Hi65 (r^2=0.95, P<0.01), Hi60 x Hi67 (r^2=0.92, P<0.05) and Hi60 x Hi26 (r^2=0.99,

Table 5.1. Mean temperature and photosynthetically active radiation among months during the effective filling period duration at Waimanalo, Hawaii.

Entry	Pedigree	PAR (moles m^{-2} day^{-1})				Temp (°C)			
		8/04	3/05	5/05	Mean	8/04	3/05	5/05	Mean
Inbreds									
Hi53	ICAL210	18.2	43.2	40.7	34.0	24.4	26.3	26.8	25.8
Hi57	Ki9	17.8	43.4	40.3	33.8	24.4	26.4	26.9	25.9
Hi60	Mo17	18.5	43.0	40.8	34.1	24.3	26.4	26.8	25.8
Hi61	N3y	17.4	42.9	40.8	33.7	24.0	26.4	26.9	25.7
Hi62	Pi17	17.2	42.3	41.3	33.6	24.1	26.4	26.9	25.8
Hi65	Tx601	17.0	42.3	41.3	33.5	24.1	26.4	26.9	25.8
Hi67	Tzi18	17.8	43.4	40.5	33.9	24.1	26.3	26.8	25.8
Hi26	Hi26	17.2	41.9	41.5	33.6	24.1	26.5	27.0	25.9
Inbred Means		17.6	42.8	40.9	33.8	24.2	26.4	26.9	25.8
Hybrids									
Hi53 x Hi57	ICAL210 x Ki9	18.9	42.9	40.1	34.0	24.3	26.3	26.8	25.8
Hi53 x Hi60	ICAL210 x Mo17	18.5	41.8	40.5	33.6	24.3	26.2	26.7	25.7
Hi53 x Hi61	ICAL210 x N3y	17.3	43.1	40.6	33.7	24.3	26.3	26.8	25.8
Hi53 x Hi62	ICAL210 x Pi17	18.7	42.4	40.2	33.8	24.3	26.3	26.8	25.8
Hi53 x Hi65	ICAL210 x Tx601	18.2	42.8	40.1	33.7	24.4	26.3	26.8	25.8
Hi53 x Hi67	ICAL210 x Tzi18	19.4	42.2	40.1	33.9	24.3	26.2	26.8	25.8
Hi53 x Hi26	ICAL210 x Hi26	17.5	42.2	40.5	33.4	24.3	26.3	26.8	25.8
Hi57 x Hi60	Ki9 x Mo17	18.7	42.5	40.3	33.8	24.3	26.2	26.8	25.8
Hi57 x Hi61	Ki9 x N3y	18.8	42.7	40.3	33.9	24.3	26.3	26.8	25.8
Hi57 x Hi62	Ki9 x Pi17	18.2	42.9	40.4	33.9	24.3	26.3	26.8	25.8
Hi57 x Hi65	Ki9 x Tx601	18.2	43.4	40.5	34.0	24.4	26.3	26.8	25.9
Hi57 x Hi67	Ki9 x Tzi18	18.5	42.5	40.3	33.8	24.3	26.2	26.8	25.8
Hi57 x Hi26	Ki9 x Hi26	18.5	42.7	40.4	33.9	24.3	26.3	26.8	25.8
Hi60 x Hi61	Mo17 x N3y	18.3	42.8	40.2	33.8	24.3	26.3	26.7	25.8
Hi60 x Hi62	Mo17 x Pi17	18.3	42.5	40.1	33.7	24.3	26.2	26.8	25.8
Hi60 x Hi65	Mo17 x Tx601	18.5	42.5	40.1	33.7	24.3	26.2	26.8	25.8
Hi60 x Hi67	Mo17 x Tzi18	19.4	42.1	40.3	33.9	24.3	26.2	26.8	25.7
Hi60 x Hi26	Mo17 x Hi26	17.8	43.3	40.6	33.9	24.4	26.3	26.8	25.8
Hi61 x Hi62	N3y x Pi17	18.5	42.2	40.7	33.8	24.3	26.3	26.8	25.8
Hi61 x Hi65	N3y x Tx601	17.5	42.2	40.3	33.4	24.3	26.3	26.9	25.8
Hi61 x Hi67	N3y x Tzi18	18.5	42.1	40.4	33.7	24.3	26.2	26.8	25.8
Hi61 x Hi26	N3y x Hi26	18.3	42.9	40.2	33.8	24.3	26.3	26.8	25.8
Hi62 x Hi65	Pi17 x Tx601	17.8	43.1	40.7	33.8	24.4	26.3	26.8	25.8
Hi62 x Hi67	Pi17 x Tzi18	18.2	43.2	40.1	33.8	24.3	26.3	26.8	25.8
Hi62 x Hi26	Pi17 x Hi26	17.3	42.9	41.1	33.8	24.3	26.3	26.8	25.8
Hi65 x Hi67	Tx601 x Tzi18	18.2	43.1	40.4	33.9	24.3	26.3	26.8	25.8
Hi65 x Hi26	Tx601 x Hi26	16.9	43.1	41.2	33.7	24.4	26.3	26.8	25.8
Hi67 x Hi26	Tzi18 x Hi26	18.3	42.9	40.2	33.8	24.3	26.3	26.8	25.8
Hybrid means		18.3	42.7	40.4	33.8	24.3	26.3	26.8	25.8
Grand Means		18.1	42.7	40.5	33.8	24.3	26.3	26.8	25.8

Table 5.2. Coefficients of determination for GFR (y) with PAR (x_1) and temperature (x_2) among inbreds and hybrids.

Entry	Pedigree	GFR (mg $k^{-1}day^{-1}$)						PAR	Temp	Array
		8/04	3/05	5/05	r^2yx_1	r^2yx_2	$r^2yx_1x_2$	x_1	x_2	Means
Inbreds										
Hi53	ICAL210	10.08	10.61	9.19	0.00	0.11	0.90		*	0.48
Hi57	Ki9	7.96	7.97	8.73	0.07	0.16	0.34			0.37
Hi60	Mo17	5.71	9.24	8.42	0.69	0.61	0.70	*		0.73
Hi61	N3y	7.57	11.96	11.11	0.93	0.82	0.95	**		0.77
Hi62	Pi17	8.33	8.56	8.07	0.0003	0.01	0.11			0.54
Hi65	Tx601	6.00	8.23	6.34	0.32	0.22	0.42			0.68
Hi67	Tzi18	6.90	6.70	7.17	0.0001	0.01	0.07			0.65
Hi26	Hi26	7.52	10.64	8.84	0.48	0.29	0.87		*	0.65
Inbred Means		7.51	9.24	8.48	0.31	0.28	0.54			
Hybrids										
Hi53 x Hi57	ICAL210 x Ki9	10.33	10.08	9.92	0.06	0.07	0.07			
Hi53 x Hi60	ICAL210 x Mo17	10.87	10.24	12.05	0.01	0.09	0.62			
Hi53 x Hi61	ICAL210 x N3y	10.76	11.37	12.13	0.41	0.60	0.71			
Hi53 x Hi62	ICAL210 x Pi17	11.32	10.44	10.15	0.34	0.38	0.38			
Hi53 x Hi65	ICAL210 x Tx601	10.13	9.14	10.71	0.03	0.00	0.45			
Hi53 x Hi67	ICAL210 x Tzi18	9.78	10.06	10.26	0.35	0.45	0.47			
Hi53 x Hi26	ICAL210 x Hi26	9.69	11.12	10.56	0.60	0.43	0.69			
Hi57 x Hi60	Ki9 x Mo17	9.53	10.30	10.60	0.27	0.30	0.30			
Hi57 x Hi61	Ki9 x N3y	10.89	11.00	12.36	0.14	0.32	0.62			
Hi57 x Hi62	Ki9 x Pi17	8.52	9.79	9.44	0.53	0.42	0.55			
Hi57 x Hi65	Ki9 x Tx601	8.48	9.14	9.21	0.22	0.22	0.23			
Hi57 x Hi67	Ki9 x Tzi18	10.15	10.16	9.39	0.08	0.19	0.39			
Hi57 x Hi26	Ki9 x Hi26	11.22	10.72	11.22	0.13	0.04	0.40			
Hi60 x Hi61	Mo17 x N3y	8.01	12.03	13.36	0.82	0.92	0.93	*		
Hi60 x Hi62	Mo17 x Pi17	9.06	10.08	10.99	0.29	0.37	0.38			
Hi60 x Hi65	Mo17 x Tx601	5.70	9.81	9.91	0.94	0.91	0.95	**		
Hi60 x Hi67	Mo17 x Tzi18	7.12	10.34	11.38	0.84	0.92	0.92	*		
Hi60 x Hi26	Mo17 x Hi26	4.70	9.64	11.51	0.86	0.98	0.99	*	*	
Hi61 x Hi62	N3y x Pi17	12.17	12.50	11.39	0.01	0.08	0.42			
Hi61 x Hi65	N3y x Tx601	8.23	11.62	10.56	0.88	0.69	0.92	*		
Hi61 x Hi67	N3y x Tzi18	10.45	10.98	12.65	0.38	0.65	0.95		**	
Hi61 x Hi26	N3y x Hi26	8.47	12.01	11.71	0.85	0.75	0.85	*		
Hi62 x Hi65	Pi17 x Tx601	9.80	9.96	8.50	0.07	0.24	0.66			
Hi62 x Hi67	Pi17 x Tzi18	8.44	9.55	9.28	0.68	0.57	0.69	*		
Hi62 x Hi26	Pi17 x Hi26	8.97	10.70	9.38	0.35	0.17	0.72			
Hi65 x Hi67	Tx601 x Tzi18	6.69	9.29	8.95	0.87	0.78	0.87	*		
Hi65 x Hi26	Tx601 x Hi26	7.16	8.88	9.18	0.68	0.70	0.70	*		
Hi67 x Hi26	Tzi18 x Hi26	10.11	9.58	10.10	0.10	0.03	0.22			
Hybrid means		9.17	10.38	10.60	0.42	0.44	0.61			
Grand Means		8.80	10.12	10.13	0.40	0.40	0.59			

P<0.05) were significantly influenced by PAR than temperature. Variation in grain filling rate of hybrid Hi61 x Hi67 (r^2=0.95, P<0.01) was attributed largely to temperature during the effective filling period duration (Table 5.2).

5.2.1.2 Grain filling period

Light accounted for most of the variation in grain filling periods among inbreds. Mean grain filling periods were shorter among inbreds and hybrids in the 8/04 planting characterized by low light and temperature as opposed to the plantings in 3/05 and 5/05 with higher levels of light and warmer temperatures (Table 5.3). Coefficients of determination for grain filing periods due to PAR and temperature varied greatly among the entries. This was 64% among inbreds and 77% among hybrids (Table 5.3). Grain filling period of inbred Hi62 a tropical flint was significantly influenced by PAR (r^2=0.81, P<0.05), while inbreds Hi61 (r^2=0.89, P<0.05) and Hi67 (r^2=0.93, P<0.05) were most responsive to temperature (Table 5.3). Array means for the multiple coefficients of determination were largest for Hi61 followed by Hi62 and Hi67.

Light was the main contributing factor to the variation in filling periods for most hybrids. Hybrids with Hi61, a highland dent were most influenced by PAR (Table 5.3). Among such hybrids were Hi53 x Hi61 (r^2=0.88, P<0.05) and Hi61 x Hi67 (r^2=0.98, P<0.01). Both PAR and temperature contributed significantly to the variations in grain filling periods for hybrids Hi61 x Hi62, Hi61 x Hi65 and Hi61 x Hi26 (Table 5.3). Variation in grain filling periods for hybrids Hi57 x Hi67 (r^2=0.86, P<0.05) and Hi62 x

Table 5.3. Coefficients of determination for GFP (y) with PAR (x_1) and temperature (x_2) among inbreds and hybrids.

Entry	Pedigree	GFP (Days)						PAR	Temp	Array
		8/04	3/05	5/05	r^2yx_1	r^2yx_2	$r^2yx_1x_2$	x_1	x_2	Means
Inbreds										
Hi53	ICAL210	27.6	29.3	33.1	0.36	0.60	0.79			0.78
Hi57	Ki9	34.4	35.6	35.9	0.14	0.17	0.17			0.68
Hi60	Mo17	26.0	27.3	34.7	0.18	0.31	0.50			0.64
Hi61	N3y	25.3	29.0	34.1	0.52	0.70	0.89		*	0.88
Hi62	Pi17	23.9	29.1	32.2	0.71	0.79	0.81	*		0.85
Hi65	Tx601	28.4	27.5	36.6	0.09	0.11	0.13			0.75
Hi67	Tzi18	25.1	29.8	32.2	0.60	0.84	0.93		*	0.81
Hi26	Hi26	19.8	26.7	32.1	0.57	0.73	0.86			0.74
Inbred Means		26.3	29.3	33.9	0.40	0.53	0.64			
Hybrids										
Hi53 x Hi57	ICAL210 x Ki9	32.6	34.6	37.5	0.38	0.55	0.64			
Hi53 x Hi60	ICAL210 x Mo17	20.7	34.2	30.5	0.89	0.72	0.94	*		
Hi53 x Hi61	ICAL210 x N3y	25.4	37.2	37.5	0.86	0.85	0.88	*		
Hi53 x Hi62	ICAL210 x Pi17	28.3	37.2	39.7	0.74	0.81	0.81	*		
Hi53 x Hi65	ICAL210 x Tx601	29.0	39.4	35.0	0.63	0.45	0.71			
Hi53 x Hi67	ICAL210 x Tzi18	29.1	32.7	36.4	0.60	0.79	0.86			
Hi53 x Hi26	ICAL210 x Hi26	27.6	33.3	37.0	0.52	0.62	0.63			
Hi57 x Hi60	Ki9 x Mo17	29.5	29.0	32.5	0.04	0.13	0.42			
Hi57 x Hi61	Ki9 x N3y	32.5	34.7	34.4	0.86	0.77	0.86	*		
Hi57 x Hi62	Ki9 x Pi17	33.1	34.4	38.4	0.22	0.41	0.63			
Hi57 x Hi65	Ki9 x Tx601	32.3	34.3	37.4	0.23	0.36	0.43			
Hi57 x Hi67	Ki9 x Tzi18	26.4	29.7	36.3	0.43	0.67	0.86		*	
Hi57 x Hi26	Ki9 x Hi26	26.9	34.0	36.3	0.81	0.89	0.89	*		
Hi60 x Hi61	Mo17 x N3y	26.8	34.5	34.5	0.50	0.51	0.51			
Hi60 x Hi62	Mo17 x Pi17	26.7	35.1	36.7	0.85	0.91	0.91	*		
Hi60 x Hi65	Mo17 x Tx601	23.6	30.4	32.3	0.71	0.78	0.78	*		
Hi60 x Hi67	Mo17 x Tzi18	25.8	28.3	32.4	0.41	0.60	0.74			
Hi60 x Hi26	Mo17 x Hi26	33.2	36.3	33.8	0.10	0.05	0.17			
Hi61 x Hi62	N3y x Pi17	22.5	34.7	40.3	0.86	0.99	0.999	*	**	
Hi61 x Hi65	N3y x Tx601	24.1	33.1	39.8	0.73	0.93	0.98	*	*	
Hi61 x Hi67	N3y x Tzi18	24.4	32.4	31.6	0.98	0.89	0.98	**		
Hi61 x Hi26	N3y x Hi26	23.2	33.1	36.5	0.86	0.98	0.98	*	*	
Hi62 x Hi65	Pi17 x Tx601	28.1	34.9	43.9	0.56	0.80	0.93		*	
Hi62 x Hi67	Pi17 x Tzi18	28.3	32.4	35.2	0.61	0.79	0.83			
Hi62 x Hi26	Pi17 x Hi26	25.6	32.8	40.0	0.59	0.77	0.87			
Hi65 x Hi67	Tx601 x Tzi18	30.9	30.7	35.3	0.07	0.22	0.55			
Hi65 x Hi26	Tx601 x Hi26	25.3	36.7	38.9	0.78	0.83	0.83	*		
Hi67 x Hi26	Tzi18 x Hi26	23.7	33.6	36.2	0.74	0.82	0.82	*		
Hybrid means		27.3	33.7	36.3	0.59	0.67	0.77			
Grand Means		27.1	32.7	35.8	0.55	0.64	0.74			

Hi65 (r^2=0.93, P<0.05) were influenced by temperature during the effective filling period duration (Table 5.3).

5.2.1.3 Kernel weight

Variations in kernel weights among inbreds and hybrids were attributed to both PAR and temperature. Kernel weights were least in the 8/04 autumn planting compared to the 3/05 and 5/05 summer plantings for inbreds and hybrids (Table 5.4). Mean kernel weights was highest in 5/05 in both inbreds and hybrids. Both temperature and light accounted for 89% of the variation in kernel weights among inbreds and 94% of the variation among hybrids (Table 5.4). Tests of significance for regression however indicate that light had the most significant contribution to the variations in kernel weights compared to temperature during the effective filling period (Table 5.4). Variation in kernel weights were greatly influenced by PAR for inbreds Hi60 (r^2=0.96, P<0.05), Hi61 (r^2=0.96, P<0.01), Hi62 (r^2=0.97, P<0.01), Hi65 (r^2=0.87, P<0.05) and Hi26 (r^2=0.98, P<0.01) (Table 5.4). These inbreds also had the highest array means for the coefficients of determination. Temperature accounted largely for kernel weight variation of Hi67 (r^2=0.99, P<0.01) (Table 5.4).

Hybrid kernel weights responded greatly to both light and temperature. Light however accounted for a greater proportion in kernel weight variations compared to temperature (Table 5.4). Significance of regression due to PAR and higher coefficients of determination were observed exclusively in hybrids Hi53 x Hi60 (r^2=0.98, P<0.01), Hi61 x Hi62 (r^2=0.98, P<0.01) and Hi62 x Hi26 (r^2=98, P<0.01) (Table 5.4). Kernel weights

Table 5.4. Coefficients of determination for kernel weight (y) with PAR (x_1) and temperature (x_2) among inbreds and hybrids.

Entry	Pedigree	Kernel weight (g)						PAR	Temp	Array
		8/04	3/05	5/05	r^2yx_1	r^2yx_2	$r^2yx_1x_2$	x_1	x_2	Means
Inbreds										
Hi53	ICAL210	139.1	155.4	151.9	0.53	0.45	0.53			0.91
Hi57	Ki9	136.7	141.6	156.3	0.34	0.60	0.88		*	0.90
Hi60	Mo17	74.0	125.7	142.5	0.88	0.96	0.96	*		0.96
Hi61	N3y	65.1	173.0	189.6	0.90	0.96	0.96	**		0.94
Hi62	Pi17	98.9	124.8	129.7	0.95	0.97	0.97	**		0.94
Hi65	Tx601	83.1	112.9	116.1	0.87	0.79	0.87	*		0.96
Hi67	Tzi18	86.0	99.8	115.4	0.56	0.85	0.99		**	0.92
Hi26	Hi26	71.6	141.9	141.4	0.98	0.95	0.98	**		0.95
Inbred Means		94.3	134.3	142.8	0.75	0.81	0.89			
Hybrids										
Hi53 x Hi57	ICAL210 x Ki9	168.1	173.6	185.7	0.34	0.59	0.82		*	
Hi53 x Hi60	ICAL210 x Mo17	112.7	174.0	183.5	0.95	0.97	0.98	**		
Hi53 x Hi61	ICAL210 x N3y	136.9	211.1	226.9	0.88	0.95	0.95	*		
Hi53 x Hi62	ICAL210 x Pi17	159.6	192.7	201.4	0.81	0.88	0.88	*		
Hi53 x Hi65	ICAL210 x Tx601	146.8	177.4	187.1	0.87	0.97	0.97	*	*	
Hi53 x Hi67	ICAL210 x Tzi18	142.3	164.6	186.7	0.64	0.84	0.92		*	
Hi53 x Hi26	ICAL210 x Hi26	133.8	184.9	194.3	0.83	0.83	0.85	*		
Hi57 x Hi60	Ki9 x Mo17	139.9	149.2	171.0	0.42	0.68	0.93		*	
Hi57 x Hi61	Ki9 x N3y	176.9	190.7	212.4	0.45	0.67	0.82			
Hi57 x Hi62	Ki9 x Pi17	141.1	167.8	181.0	0.71	0.85	0.87	*		
Hi57 x Hi65	Ki9 x Tx601	135.6	156.5	171.9	0.73	0.94	0.997	*	**	
Hi57 x Hi67	Ki9 x Tzi18	134.0	150.4	170.2	0.56	0.78	0.89		*	
Hi57 x Hi26	Ki9 x Hi26	150.6	182.1	203.3	0.75	0.92	0.96	*	*	
Hi60 x Hi61	Mo17 x N3y	106.9	206.2	230.3	0.88	0.96	0.96	*		
Hi60 x Hi62	Mo17 x Pi17	119.8	176.8	201.3	0.82	0.94	0.95	*		
Hi60 x Hi65	Mo17 x Tx601	66.7	134.7	159.9	0.80	0.90	0.91	*		
Hi60 x Hi67	Mo17 x Tzi18	92.1	146.1	183.7	0.77	0.96	0.995	*	**	
Hi60 x Hi26	Mo17 x Hi26	68.9	175.2	194.5	0.94	0.99	0.997	**	**	
Hi61 x Hi62	N3y x Pi17	137.1	216.6	229.6	0.94	0.98	0.98	**		
Hi61 x Hi65	N3y x Tx601	99.5	192.5	209.9	0.92	0.97	0.98	**	*	
Hi61 x Hi67	N3y x Tzi18	115.4	177.8	200.0	0.83	0.92	0.92	*		
Hi61 x Hi26	N3y x Hi26	97.7	199.1	213.5	0.95	0.97	0.99	**	*	
Hi62 x Hi65	Pi17 x Tx601	136.9	174.0	185.9	0.87	0.98	0.98	*	*	
Hi62 x Hi67	Pi17 x Tzi18	119.6	154.5	162.7	0.87	0.95	0.95	*		
Hi62 x Hi26	Pi17 x Hi26	114.7	175.6	186.3	0.94	0.98	0.98	**		
Hi65 x Hi67	Tx601 x Tzi18	103.5	142.1	157.9	0.75	0.88	0.89	*		
Hi65 x Hi26	Tx601 x Hi26	88.9	162.6	178.3	0.94	0.99	0.993	**	*	
Hi67 x Hi26	Tzi18 x Hi26	119.3	160.3	182.7	0.72	0.89	0.91	*		
Hybrid means		123.7	173.9	191.1	0.78	0.90	0.94			
Grand Means		117.2	165.1	180.4	0.77	0.88	0.93			

of some hybrids were also significantly influenced by both light and temperature (Table 5.4). Regressions due to light and temperature were both significant (r^2=0.997, P<0.01) for Hi60 x Hi26.

5.2.1.4 Plant yield

Light compared to temperature had the greatest effect on plant yields for both inbreds and hybrids. Plant yields among inbreds were least in the autumn planting in 8/04 and were highest in the summer plantings in 3/05 and 5/05. Coefficients of determination varied greatly among inbreds which improved when both light and temperature were used in the calculation of the multiple regressions (Table 5.5). Light alone was the major factor that accounted for the differences in plant yields for inbreds Hi60 (r^2=0.89, P<0.05), Hi61 (r^2=0.88, P<0.05), Hi62 (r^2=0.94, P<0.05), Hi65 (r^2=0.97, P<0.01) (Table 5.5). Plant yields for inbreds Hi53, Hi57 and Hi67 were significantly influenced by both light and temperature. Array means for coefficients of determination was largest for Hi61.

Hybrid entries responded differently to PAR and temperature. Mean hybrid plant yields were lowest in the 8/04 trial under low PAR and temperature, and were highest in the 3/05 and 5/05 plantings characterized by high PAR and temperature (Table 5.5). Light as opposed to temperature was the major factor that contributed significantly to the variations in most hybrid plant yields. Tests for significance of regression also showed that variation in plant yields for hybrids Hi53 x Hi65, Hi53 x Hi67, Hi60 x Hi67 and Hi62 x Hi26 were attributed to both PAR and temperature (Table 5.5).

Table 5.5. Coefficients of determination for plant yield (y) with PAR (x_1) and temperature (x_2) among inbreds and hybrids.

Entry	Pedigree	Plant yield (g)						PAR	Temp	Array
		8/04	3/05	5/05	r^2yx_1	r^2yx_2	$r^2yx_1x_2$	x_1	x_2	Means
Inbreds										
Hi53	ICAL210	14.1	24.0	20.4	0.92	0.69	0.99	*	*	0.94
Hi57	Ki9	17.8	28.0	30.2	0.91	0.98	0.98	**	*	0.90
Hi60	Mo17	7.3	17.4	17.3	0.88	0.87	0.89	*		0.89
Hi61	N3y	5.2	23.3	22.3	0.87	0.86	0.88	*		0.95
Hi62	Pi17	11.5	22.1	20.0	0.91	0.80	0.94	*		0.85
Hi65	Tx601	4.5	25.7	21.5	0.96	0.86	0.97	**		0.94
Hi67	Tzi18	13.7	22.2	24.1	0.91	0.99	0.995	**	**	0.94
Hi26	Hi26	4.8	14.0	12.8	0.79	0.75	0.79	*		0.94
Inbred Means		9.9	22.1	21.1	0.89	0.85	0.93			
Hybrids										
Hi53 x Hi57	ICAL210 x Ki9	30.4	44.7	43.8	0.90	0.85	0.91	**		
Hi53 x Hi60	ICAL210 x Mo17	20.6	44.0	43.2	0.97	0.90	0.97	**		
Hi53 x Hi61	ICAL210 x N3y	21.6	53.1	52.2	0.96	0.91	0.96	**		
Hi53 x Hi62	ICAL210 x Pi17	29.7	46.5	45.1	0.97	0.88	0.97	**		
Hi53 x Hi65	ICAL210 x Tx601	28.9	51.5	42.2	0.88	0.63	0.98	*	*	
Hi53 x Hi67	ICAL210 x Tzi18	25.6	42.0	50.7	0.78	0.93	0.95	*	*	
Hi53 x Hi26	ICAL210 x Hi26	24.1	48.9	45.9	0.82	0.72	0.83	*		
Hi57 x Hi60	Ki9 x Mo17	30.4	36.2	44.1	0.53	0.76	0.90		*	
Hi57 x Hi61	Ki9 x N3y	27.6	46.5	47.6	0.91	0.91	0.93	**		
Hi57 x Hi62	Ki9 x Pi17	29.7	43.8	43.7	0.71	0.70	0.72	*		
Hi57 x Hi65	Ki9 x Tx601	36.1	54.3	50.3	0.90	0.77	0.91	**		
Hi57 x Hi67	Ki9 x Tzi18	30.2	44.3	48.2	0.86	0.93	0.93	*		
Hi57 x Hi26	Ki9 x Hi26	32.3	49.6	48.2	0.97	0.89	0.97	**		
Hi60 x Hi61	Mo17 x N3y	11.0	42.4	42.3	0.98	0.95	0.99	**		
Hi60 x Hi62	Mo17 x Pi17	21.2	41.7	27.4	0.26	0.14	0.42			
Hi60 x Hi65	Mo17 x Tx601	12.6	37.8	42.6	0.91	0.96	0.96	**		
Hi60 x Hi67	Mo17 x Tzi18	20.0	36.3	46.5	0.79	0.96	0.99	*	**	
Hi60 x Hi26	Mo17 x Hi26	13.5	48.4	44.5	0.99	0.89	0.99	**		
Hi61 x Hi62	N3y x Pi17	22.4	47.1	44.2	0.97	0.88	0.97	**		
Hi61 x Hi65	N3y x Tx601	12.4	46.0	50.1	0.94	0.96	0.97	**		
Hi61 x Hi67	N3y x Tzi18	22.5	44.9	46.8	0.92	0.91	0.93	**		
Hi61 x Hi26	N3y x Hi26	14.9	41.9	43.7	0.88	0.87	0.90	*		
Hi62 x Hi65	Pi17 x Tx601	26.2	50.8	45.4	0.92	0.78	0.93	**		
Hi62 x Hi67	Pi17 x Tzi18	23.8	39.1	37.4	0.94	0.86	0.94	**		
Hi62 x Hi26	Pi17 x Hi26	21.9	43.9	47.0	0.96	0.99	0.99	**	*	
Hi65 x Hi67	Tx601 x Tzi18	23.4	40.7	48.0	0.77	0.90	0.91	*		
Hi65 x Hi26	Tx601 x Hi26	19.0	51.1	52.9	0.91	0.89	0.92	**		
Hi67 x Hi26	Tzi18 x Hi26	28.1	44.2	50.2	0.83	0.95	0.95	*		
Hybrid means		23.6	45.1	45.5	0.86	0.85	0.92			
Grand Means		20.5	40.0	40.1	0.87	0.85	0.92			

5.2.1.5 Kernel numbers

Variation in kernel numbers was greatly influenced by light and temperature among inbreds and hybrids (Table 5.6). Mean kernel numbers were lowest in 8/04 autumn planting under low light and temperature and were similar in the 3/05 and 5/05 summer trials. Kernel numbers increased with increasing PAR and temperatures. In 8/04, mean kernel numbers was 19.9 which increased to 27.3 in 3/05 and 27.6 in 5/05. Coefficients of determination varied significantly among inbred and hybrid entries. Both PAR and temperature accounted for similar variations in kernel numbers among inbreds and hybrids. Light accounted for a larger proportion of the variation among inbreds. Variation in variation in kernel numbers for inbreds Hi57 (r^2=0.96, P<0.01) and Hi67 (r^2=0.94, P<0.01) were explained largely by light (Table 5.6). Array means were highest for Hi67, followed by Hi53 and Hi60.

Variations in kernel numbers among hybrids were also accounted largely by PAR as opposed to temperature. Mean kernel numbers were least during the 8/04 planting and were higher during the summer plantings in 3/05 and 5/05 (Table 5.6). Coefficients of determination increased when PAR and temperature were used in the calculation of multiple regressions. Regressions due to PAR as opposed to temperature were significant for most hybrids. Variation in kernel numbers for hybrids Hi53 x Hi67, Hi57 x Hi60 and Hi60 x Hi65 were attributed to both PAR and temperature (Table 5.6). Temperature explained most of the variation in kernel numbers for hybrids Hi65 x Hi67 and Hi67 x Hi26.

Table 5.6. Coefficients of determination for kernel number (y) with PAR (x_1) and temperature (x_2) among inbreds and hybrids.

Entry	Pedigree	Kernel number						PAR	Temp	Array
Hybrids		8/04	3/05	5/05	r^2yx_1	r^2yx_2	$r^2yx_1x_2$	x_1	x_2	Means
Inbreds										
Hi53	ICAL210	19.4	25.1	25.1	0.82	0.79	0.83	*		0.89
Hi57	Ki9	20.7	28.6	29.3	0.93	0.94	0.96	**		0.81
Hi60	Mo17	24.3	28.4	27.5	0.52	0.43	0.55			0.89
Hi61	N3y	17.2	28.8	30.2	0.86	0.91	0.91	*		0.84
Hi62	Pi17	22.2	26.9	28.5	0.82	0.89	0.90	*		0.86
Hi65	Tx601	16.2	31.9	26.8	0.87	0.78	0.88	*		0.83
Hi67	Tzi18	24.7	30.2	31.7	0.90	0.94	0.94	**		0.91
Hi26	Hi26	14.4	18.6	21.5	0.63	0.71	0.74			0.86
Inbred Means		19.9	27.3	27.6	0.79	0.80	0.84			
Hi53 x Hi57	ICAL210 x Ki9	24.4	34.0	32.6	0.91	0.82	0.91	**		
Hi53 x Hi60	ICAL210 x Mo17	34.1	44.1	39.9	0.77	0.56	0.91	*		
Hi53 x Hi61	ICAL210 x N3y	30.6	40.9	39.1	0.69	0.59	0.69	*		
Hi53 x Hi62	ICAL210 x Pi17	26.9	34.9	34.4	0.89	0.83	0.90	**		
Hi53 x Hi65	ICAL210 x Tx601	29.6	40.4	34.8	0.73	0.47	0.90	*		
Hi53 x Hi67	ICAL210 x Tzi18	25.0	35.9	38.9	0.90	0.98	0.98	**	*	
Hi53 x Hi26	ICAL210 x Hi26	28.1	37.1	36.8	0.96	0.90	0.96	**		
Hi57 x Hi60	Ki9 x Mo17	32.5	39.6	42.5	0.82	0.94	0.95	**	*	
Hi57 x Hi61	Ki9 x N3y	25.9	36.2	36.0	0.93	0.90	0.94	**		
Hi57 x Hi62	Ki9 x Pi17	28.9	36.5	36.3	0.85	0.81	0.86	*		
Hi57 x Hi65	Ki9 x Tx601	34.6	40.3	37.2	0.36	0.23	0.44			
Hi57 x Hi67	Ki9 x Tzi18	29.7	35.3	35.8	0.78	0.78	0.80	*		
Hi57 x Hi26	Ki9 x Hi26	30.4	39.2	37.1	0.77	0.63	0.79	*		
Hi60 x Hi61	Mo17 x N3y	27.4	43.7	43.6	0.79	0.74	0.79	*		
Hi60 x Hi62	Mo17 x Pi17	32.0	41.2	41.3	0.77	0.76	0.79	*		
Hi60 x Hi65	Mo17 x Tx601	31.9	43.9	46.8	0.91	0.98	0.99	**	*	
Hi60 x Hi67	Mo17 x Tzi18	36.5	39.5	42.2	0.62	0.81	0.87			
Hi60 x Hi26	Mo17 x Hi26	32.3	45.7	43.2	0.93	0.80	0.94	**		
Hi61 x Hi62	N3y x Pi17	32.3	38.4	37.1	0.86	0.74	0.87	*		
Hi61 x Hi65	N3y x Tx601	24.1	36.8	39.2	0.81	0.86	0.86	*		
Hi61 x Hi67	N3y x Tzi18	29.4	37.3	37.4	0.91	0.88	0.92	**		
Hi61 x Hi26	N3y x Hi26	28.8	38.9	37.5	0.80	0.71	0.80	*		
Hi62 x Hi65	Pi17 x Tx601	30.2	40.2	36.0	0.77	0.56	0.85	*		
Hi62 x Hi67	Pi17 x Tzi18	29.1	36.0	36.3	0.91	0.91	0.93	**		
Hi62 x Hi26	Pi17 x Hi26	35.7	41.5	41.6	0.86	0.83	0.86	*		
Hi65 x Hi67	Tx601 x Tzi18	33.1	35.4	40.6	0.43	0.72	0.98		**	
Hi65 x Hi26	Tx601 x Hi26	33.8	42.0	44.4	0.75	0.80	0.80	*		
Hi67 x Hi26	Tzi18 x Hi26	34.1	37.4	41.0	0.55	0.78	0.89		*	
Hybrid means		30.4	39.0	38.9	0.79	0.76	0.86			
Grand Means		28.07	36.41	36.39	0.79	0.77	0.86			

5.2.1.5 Kernel row numbers

Mean kernel row numbers among hybrids were consistent among the three planting dates despite differences in light and temperature among the autumn and summer trials (Table 5.7). Differences in mean kernel row numbers among hybrids were less apparent among planting dates. This was reflected in the analysis of variance for kernel row numbers (Chapter 7) that showed no significant differences in the hybrid x month interaction. Light and temperature explained 47.0% of the variation only in kernel row numbers. Temperature accounted largely for the variation in kernel row numbers specifically among inbreds Hi65 (r^2=0.98, P<0.01) and Hi26 (r^2=0.97, P<0.01). Kernel row number was established during the first 30 days of growth and hence PAR and temperatures during the effective filling period duration did not correlate well with kernel row numbers.

Table 5.7. Coefficients of determination for kernel row number (y) with PAR (x_1) and temperature (x_2) among inbreds and hybrids.

Entry	Pedigree	Kernel row number						PAR	Temp	Array
Hybrids		8/04	3/05	5/05	r^2yx_1	r^2yx_2	$r^2yx_1x_2$	x_1	x_2	Means
Inbreds										
Hi53	ICAL210	12.5	11.9	13.2	0.00	0.04	0.73		*	0.34
Hi57	Ki9	13.8	14.4	15.4	0.18	0.30	0.42			0.41
Hi60	Mo17	9.8	10.0	10.5	0.23	0.39	0.67			0.53
Hi61	N3y	8.8	10.0	9.8	0.54	0.54	0.55			0.40
Hi62	Pi17	12.4	13.0	13.2	0.31	0.31	0.32			0.38
Hi65	Tx601	10.8	15.4	16.0	0.95	0.97	0.98	**		0.47
Hi67	Tzi18	15.0	15.7	14.2	0.00	0.05	0.79		*	0.37
Hi26	Hi26	11.4	12.7	12.8	0.93	0.97	0.97	**		0.37
Inbred Means		11.8	12.9	13.1	0.39	0.45	0.68			
Hi53 x Hi57	ICAL210 x Ki9	14.2	14.6	15.0	0.29	0.38	0.42			
Hi53 x Hi60	ICAL210 x Mo17	12.4	12.2	13.2	0.04	0.12	0.39			
Hi53 x Hi61	ICAL210 x N3y	12.6	12.8	13.6	0.07	0.14	0.22			
Hi53 x Hi62	ICAL210 x Pi17	13.8	13.2	13.8	0.08	0.02	0.22			
Hi53 x Hi65	ICAL210 x Tx601	14.6	14.6	14.2	0.04	0.09	0.19			
Hi53 x Hi67	ICAL210 x Tzi18	14.6	14.2	14.8	0.02	0.00	0.22			
Hi53 x Hi26	ICAL210 x Hi26	13.0	14.0	14.9	0.52	0.68	0.73			
Hi57 x Hi60	Ki9 x Mo17	13.6	12.8	13.6	0.13	0.04	0.40			
Hi57 x Hi61	Ki9 x N3y	12.8	13.2	13.8	0.18	0.26	0.30			
Hi57 x Hi62	Ki9 x Pi17	15.0	14.4	14.8	0.12	0.06	0.19			
Hi57 x Hi65	Ki9 x Tx601	15.4	16.2	16.4	0.63	0.71	0.71			
Hi57 x Hi67	Ki9 x Tzi18	15.6	15.6	16.8	0.14	0.35	0.74			
Hi57 x Hi26	Ki9 x Hi26	14.0	13.4	13.8	0.04	0.02	0.08			
Hi60 x Hi61	Mo17 x N3y	9.8	10.6	11.1	0.69	0.82	0.84	*		
Hi60 x Hi62	Mo17 x Pi17	12.4	11.6	12.4	0.33	0.09	0.995		**	
Hi60 x Hi65	Mo17 x Tx601	12.8	12.3	13.0	0.09	0.00	0.75		*	
Hi60 x Hi67	Mo17 x Tzi18	12.8	13.2	13.6	0.18	0.24	0.26			
Hi60 x Hi26	Mo17 x Hi26	12.5	12.8	12.4	0.02	0.00	0.10			
Hi61 x Hi62	N3y x Pi17	12.0	11.8	12.0	0.03	0.01	0.08			
Hi61 x Hi65	N3y x Tx601	12.3	13.4	13.6	0.57	0.58	0.59			
Hi61 x Hi67	N3y x Tzi18	13.2	12.6	13.6	0.01	0.01	0.48			
Hi61 x Hi26	N3y x Hi26	11.8	11.4	12.4	0.00	0.03	0.29			
Hi62 x Hi65	Pi17 x Tx601	13.6	14.4	14.4	0.35	0.33	0.35			
Hi62 x Hi67	Pi17 x Tzi18	14.6	14.6	14.0	0.05	0.13	0.30			
Hi62 x Hi26	Pi17 x Hi26	12.2	12.0	13.2	0.05	0.16	0.52			
Hi65 x Hi67	Tx601 x Tzi18	15.6	15.2	15.8	0.02	0.00	0.22			
Hi65 x Hi26	Tx601 x Hi26	13.8	14.8	15.0	0.50	0.50	0.51			
Hi67 x Hi26	Tzi18 x Hi26	14.2	14.8	15.0	0.35	0.37	0.37			
Hybrid means		13.4	13.5	13.9	0.20	0.22	0.41			
Grand Means		13.05	13.33	13.75	0.24	0.27	0.47			

5.3 Discussions

Photosynthetic active radiation as opposed to temperature accounted for greater significance of the variations in the agronomic traits studied among inbreds and hybrids across the three Waimanalo planting dates. The temperature differences among the planting dates were relatively small compared to PAR. Light values were 50% more during the summer plantings in 3/05 and 5/05 compared to the autumn planting in 8/04. Since PAR and temperature are understood to be inseparable and highly correlated, multiple regression analysis was used to determine the relationships between the climatic factors and the agronomic traits. Coefficients of determination greatly improved when both PAR and temperature were used in the regression calculations as opposed to using the climatic factors independently.

Temperature and PAR during the effective filling period duration accounted for 54.0% of the variation in grain filling rates among inbreds and 61.0% of the variation among hybrids. Grain filling rates increased with increasing PAR and temperature. Photosynthetic active radiation as opposed to temperature accounted for greater significance of the variations in grain filling rates among entries. Variation in GFR for inbred Hi61 a highland tropical dent was accounted largely by PAR (95.0%). Tropical inbreds Hi62 and Hi67 had consistent GFR among the three planting dates and had the least coefficients of determination. Tropical inbreds Hi62 and Hi67 did not respond to the changes in PAR and temperature between the autumn and summer plantings. Rates of fill for hybrid Hi60 x Hi26 were significantly affected by light and temperature.

The effects of temperature were less apparent on grain filling rates which was consistent with previous reports. Mean temperature differences were small compared to the autumn and summer plantings in Waimanalo. This difference was 2°C between the trial in 8/04 and in 2005. Across years (2003-2005), the difference between the maximum and minimum mean monthly temperature readings was 4.6°C (Figure 2.1). As reported in previous studies, grain filling rates were not affected by temperature in maize (Badu-Apraku et al., 1983), wheat (Ford and Thorne, 1975) and in rice (Kobata and Uemuki, 2004). Under controlled environments, Badu-Apraku et al. (1983) reported the effects of different day and night temperature regimes on grain filling rate on a single cross maize hybrid, Guelph GX 122 in a two year study. Day and night temperature controls in each growth cabinet were, 25/15, 25/25, 35/15 and 35/25 (°C). Despite the large differences between day and night temperatures, and between temperature treatments, mean kernel growth rates in each treatment were not significantly different. For the trials planted in Waimanalo, mean differences between the highest and lowest GFR were quite small between the autumn and summer plantings. These differences were 1.73 mg kernel^{-1} day^{-1} among inbreds, and 0.9 mg kernel^{-1} day^{-1} among hybrids. In comparison to the study of Badu-Apraku et al. (1983), the difference between the highest and lowest kernel growth rate of Guelph GX 122 was only 0.5 mg day^{-1}. Contrary to the above reports and this study at Waimanalo, Muchow et al. (1990) at the Katherine Research Station with a temperature range of 25.4 to 31.6°C in northern Australia reported a significant correlation between the rate of grain growth and temperature

(r^2=0.82, P<0.05) in a maize hybrid Dekalb XL82 among five different planting dates under relatively constant amounts of light.

Photosynthetic active radiation accounted for larger proportions of the variation in grain filling periods among inbreds and hybrids. On average, PAR and temperature accounted for 64% of the variation in grain filling periods among inbreds and 77% of the variation among hybrids. Regressions due to light as opposed to temperature however were significant for most inbreds and hybrids. In contrast to the significant effects of PAR on grain filling periods in this study, Tollenaar (1999) under controlled growth conditions using different photoperiods and photosynthetic photon flux densities (PPFD) reported no significant differences in duration of grain filling from silking to half milk line (33.1 to 33.8 days) and from silking to black layer formation (41.3 to 41.7 days) on a short season maize hybrid Pioneer 3902. The treatments consisted of (1) 10h photoperiod with high PPFD (650 μmol m^{-2} s^{-1}), (2) 20h photoperiod consisting of 10h of high PPFD followed by 10h or low PPFD (5-50 μmol m^{-2} s^{-1}), and (3) a 20h photoperiod of high PPFD.

Regressions due to temperature effects were less apparent on grain filling periods among inbreds and hybrids. Longer effective grain filling period durations resulted for the inbreds and hybrids planted in Waimanalo under the higher temperature planting dates in 3/05 and 5/05 than in the low temperature season in 8/04. For all entries, shortest mean GFP (27.12) was in 8/04 (24.2°C) while longest mean GFP (36.3) was in 5/05 (26.8°C). Badu-Apraku et al. (1983) under controlled growth conditions reported a longer duration of the linear phase of growth (25 days) at lower temperatures (25/15) and

shorter duration (10 days) at a higher temperature treatment (35/25), a GFP difference of 15 days and a temperature difference of 10°C. Under Waimanalo conditions, the average temperature difference was 2°C between the 8/04 and 2005 planting dates. The difference between the longest and shortest mean GFP (8/04 vs. 5/05) was 7.6 days among inbreds, and 8.7 days among hybrids. The mean temperature during the effective filling period duration across the three Waimanalo planting dates was 25.8°C which accounted only for half of the variation in filling periods among inbreds and hybrids. Contrary to the less effects of temperature on grain filling rates in Waimanalo, Muchow (1990) in northern Australia reported a significant coefficient of determination (r^2=0.95, P<0.01) between the reciprocal of the effective filling period and temperature. With the very small differences in mean temperature and large differences in light values among the planting dates at Waimanalo compared to northern Australia with large differences in temperature and relative constant amounts of light (927-997 MJ m^{-2}) among planting dates, it is clear that light accounted for the major differences in grain filling periods in Waimanalo.

Light as opposed to temperature accounted also for greater variations in kernel weights and plant yields among inbreds and hybrids. Among inbreds, variations in these traits due to PAR and temperatures were 89% for kernel weight and 93% for plant yield. Among hybrids, this was 94% for kernel weight and 92% for plant yield. Regressions due to light were mostly significant for inbreds and hybrids. This corroborates to the study of Jong et al. (1982) which obtained a significant and higher correlation coefficient (r=0.768, P<0.01) between maize grain yield and average daily solar radiation (cal cm^{-2}

day^{-1}) as opposed to temperature (r=0.599, P<0.01) in a series of 41 monthly plantings at Waimanalo, Hawaii. In contrast to the predominating effects of light on kernel weights in this study, Tollenaar (1999) reported that incident photosynthetic photon flux density had no significant effects on kernel weights (during half milk line and black layer) of a short season maize hybrid Pioneer 3902 under controlled growth conditions.

Mean kernel weights and plant yields increased under high temperatures in 3/05 and 5/05. In a related study on the effects of temperature, Badu-Apraku (1983) reported lower grain weights per plant at extremely high day/night temperatures (35/25 = 69.0g) than lower temperatures (25/15=124g) under controlled planting dates. Contrary to this report, Muchow et al. (1990) in northern Australia found that grain yield was not significantly correlated with temperature per se despite a wide range of temperature differences among five planting dates (25.4°C-31.6°C). In this current study, mean temperatures during the effective filling period in Waimanalo during the summer plantings however did not exceed 27°C. Because of the relatively small differences in temperatures among the three Waimanalo planting dates, the effects of much higher temperatures on kernel weight and plant yield could not be determined. It is clear however that light was the major factor that caused the differences in kernel weights and plant yields.

Light also accounted for most of the variation in kernel numbers. Kernel numbers per row among inbreds and hybrids were lower in 8/04 and increasing in 3/05 and 5/05 under higher and similar PAR and temperature conditions. Light and temperature accounted for 84% variation in kernel numbers among inbreds and 86% of the variation

among hybrids, respectively. Tollenaar (1999) reported that incident photosynthetic photon flux density had no significant effects also on kernel numbers per ear, for a short season maize hybrid Pioneer 3902 under controlled growth conditions. However for this study at Waimanalo, it was clear that variation in kernel numbers were mainly due to the effects of light. A high correlation between average daily solar radiation and kernels per ear (r=0.717, P<0.01) in maize was also reported by Jong et al. (1982) in Waimanalo.

Kernel row numbers were less influenced by light and temperature during the effective filling period duration. This is because the initiation of kernel row numbers takes place during the first 30 days of growth.

CHAPTER 6
DIALLEL ANALYSIS OF CHLOROPHYLL CONCENTRATION IN MAIZE

6.1 Introduction

Previous studies have shown that maize grain yield was correlated with chlorophyll concentration (Sprague and Curtis, 1933; Everett, 1960). Crosbie et al. (1978) proposed that improvement of photosynthetic efficiency could increase the yield potential of maize. Large additive genetic variances for photosynthesis measured as CO_2-exchange rates in maize were reported by Crosbie et al. (1977, 1978). Piekielek and Fox (1992) reported that chlorophyll concentration is also an indicator of nitrogen levels. Nitrogen metabolism in the leaves is related to the stay-green characteristic in maize that is associated with longer photosynthetic period and increased grain yield. D'Croz-Mason and Lindauer (1997) reported that chlorophyll concentration was also a good indicator of the stay-green characteristic. Richards (2000) reported that a genetic increase in the rate of photosynthesis per unit leaf area had not yet been achieved in corn, mainly because of increased use and dependence on nitrogen fertilizers. Nitrogen increases leaf area, leaf area duration and leaf nitrogen content, all of which result in an increase in photosynthesis per unit ground area. Under these favorable conditions, selection pressure for plants with increased photosynthetic rate becomes ineffective since higher rates of photosynthesis per unit ground area have already been achieved.

The objectives of this study were to (1) measure genetic variation and genotype by planting date interactions for chlorophyll concentration measured as SPAD and (2) to estimate general combining ability (GCA) and specific combining ability (SCA) effects for chlorophyll concentration and the interaction of these effects with the planting date.

Eight elite inbreds were crossed in a diallel without reciprocals (Griffing, 1956). The 28 diallel hybrids used for this study were described previously in Chapter 2. Diallel trials were planted in July 7, 2004 (7/04), August 30, 2004 (8/04), March 16, 2005 (3/05) and in May 15, 2005 (5/05). Chlorophyll concentration was measured using a SPAD meter developed by Minolta Corp. This meter allows measurement of chlorophyll concentration without destructive tissue sampling. A total of 3 readings were taken throughout the life cycle in each trial. Readings were first taken at 30 days after planting (DAP) which was around the 8-10 leaf stage, then at 60 DAP during anthesis and silking, and at 90 DAP approximately during the hard dough stage (R4) (Chapter 1). Measurements taken at 30 DAP were from the middle of youngest fully expanded leaf, while measurements at 60 and 90 DAP were taken from the middle of the leaf subtending the tassel. A total of ten plants per plot were sampled for SPAD. For consistency, SPAD readings were taken during the day between 10:00 AM to 2:00 PM.

6.2 Results

6.2.1 Mean performance and analysis of variance

Table 6.1 summarizes SPAD readings at 30, 60 and 90 days after planting for the 8 inbreds and 28 hybrids planted in 2004 and 2005. Mean SPAD were lowest at 30 DAP (27.40), highest at 60 DAP (45.7) decreasing at 90 DAP (41.2). Average SPAD values among inbreds in the 7/04 planting were 27.5 (30 DAP), 46.7 (60 DAP) and 37.1 (90 DAP) (Table 6.1). In the low PAR 8/4 planting date, SPAD averaged 26.5 at 30 DAP, 45.7 at 60 DAP and 41.5 at 90 DAP. In the 3/04 planting date, the mean SPAD readings were 24.4 at 30 DAP, 37.4 and 45.2 for 60 and 90 DAP. For the 5/05 trial, the SPAD means among inbreds were 29.2, 35.8, for 30 and 60 DAP, respectively and 30.7 at 90 DAP. Mean SPAD values varied greatly among inbreds in the three growth stages. At 30 DAP, SPAD ranged from 31.8 (Hi53) to 23.1 (Hi65). At 60 DAP, SPAD ranged from 36.3 (Hi62) to 48.9 (Hi60), and at 90 DAP, SPAD ranged from 37.0 (Hi61) to 41.0 (Hi53).

Mean chlorophyll concentrations of hybrids also were lowest at 30 DAP, and higher during anthesis and silking (60 DAP), decreasing during the hard dough stage (90 DAP) (Table 6.1). At 30 DAP mean SPAD values were 26.0, 29.4, 25.5, 28.6, for the 7/04, 8/04, 3/05, and 5/05 planting dates, respectively. At 60 DAP, mean SPAD readings were 51.58 for 7/04, 51.09 for 8/04 and 39.05 and 46.06 for the 3/04 and 5/05 trials, respectively. At 90 DAP, the mean SPAD readings for hybrids were 41.6, 43.8, 45.2 and 37.4 for each of the four planting dates. Mean SPAD for all hybrids across planting dates were 27.5, 39.2, and 41.0 at 30, 60 and 90 DAP, respectively.

Table 6.1. Mean SPAD readings of hybrids and inbreds taken at 30, 60, 90 DAP within and across planting dates.

Entries	7/04			8/04			3/05			5/05			Mean		
	30	60	90	30	60	90	30	60	90	30	60	90	30	60	90
Inbreds															
Hi53	32.1	52.6	46.4	31.4	41.3	42.4	30.6	33.7	48.6	33.0	29.1	26.8	31.8	39.2	41.0
Hi57	27.6	40.9	33.5	28.3	43.7	43.1	24.1	39.3	43.2	27.1	35.7	32.8	26.8	39.9	38.1
Hi60	24.9	54.9	38.5	26.9	56.2	39.3	24.0	39.0	45.0	30.0	45.5	36.0	26.4	48.9	39.7
Hi61	26.1	46.0	38.8	20.6	44.1	35.0	24.2	34.0	44.8	26.1	38.1	29.4	24.2	40.5	37.0
Hi62	31.2	40.1	38.4	33.4	37.5	42.4	24.5	46.6	47.5	36.0	23.2	27.5	31.3	36.8	39.0
Hi65	27.6	46.6	31.7	20.4	48.1	42.9	19.7	32.4	46.5	24.6	32.2	30.3	23.1	39.8	37.9
Hi67	23.9	48.8	32.3	26.4	44.0	39.0	22.8	38.8	42.1	25.1	41.7	29.4	24.6	43.3	35.7
Hi26	26.3	43.7	37.0	24.9	50.6	47.5	25.5	35.1	43.5	31.8	41.2	33.9	27.1	42.6	40.5
Inbred means	27.5	46.7	37.1	26.5	45.7	41.4	24.4	37.4	45.1	29.2	35.8	30.8	26.9	41.4	38.6
Hybrids															
Hi53 x Hi57	28.1	49.1	44.3	28.7	46.1	44.4	28.0	37.9	41.3	31.0	41.3	37.1	28.9	43.6	41.8
Hi53 x Hi60	27.3	56.8	46.2	32.1	54.2	45.1	29.8	41.1	49.7	31.0	45.9	40.1	30.0	49.5	45.3
Hi53 x Hi61	24.2	50.2	41.7	31.1	53.9	46.7	26.2	31.1	44.2	27.7	45.3	35.8	27.3	45.1	42.1
Hi53 x Hi62	28.7	49.1	44.1	32.8	52.6	43.7	29.1	32.8	42.4	29.5	44.5	37.9	30.0	44.7	42.0
Hi53 x Hi65	25.7	49.7	37.9	27.1	48.6	45.9	28.7	35.3	39.8	28.2	41.5	36.8	27.4	43.8	40.1
Hi53 x Hi67	28.5	49.8	42.9	30.9	45.4	39.5	26.6	38.6	41.7	29.4	44.4	33.3	28.8	44.5	39.3
Hi53 x Hi26	28.9	53.7	38.6	29.7	54.5	50.7	28.7	43.3	45.9	26.3	50.6	39.0	28.4	50.5	43.5
Hi57 x Hi60	27.4	54.7	41.8	28.9	52.2	48.5	24.6	41.8	47.9	30.7	47.2	37.2	27.9	49.0	43.8
Hi57 x Hi61	26.3	46.9	38.0	28.0	45.5	38.8	25.7	35.0	37.6	26.9	40.3	31.4	26.7	41.9	36.5
Hi57 x Hi62	26.5	46.5	42.0	30.9	47.1	41.7	30.1	32.3	43.3	29.7	39.6	35.1	29.3	41.4	40.5
Hi57 x Hi65	26.0	49.7	41.0	27.1	48.5	47.9	25.1	33.0	46.9	25.6	45.1	34.0	26.0	44.1	42.5
Hi57 x Hi67	29.7	48.7	41.5	28.9	52.8	46.3	23.1	38.2	45.7	29.1	42.0	35.0	27.7	45.4	42.1
Hi57 x Hi26	25.2	52.3	43.0	30.1	51.4	48.2	22.6	41.3	47.8	25.2	50.3	39.1	25.8	48.8	44.5
Hi60 x Hi61	27.1	57.4	44.2	28.0	54.8	38.3	28.7	46.2	49.1	28.8	51.5	45.7	28.1	52.5	44.3
Hi60 x Hi62	28.7	55.8	41.4	32.5	54.4	41.6	29.0	35.6	44.7	27.5	52.2	39.4	29.4	49.5	41.8
Hi60 x Hi65	26.6	57.1	43.4	30.6	53.5	42.7	22.3	42.8	46.0	27.9	50.9	35.2	26.8	51.0	41.8
Hi60 x Hi67	25.1	58.1	45.7	28.3	55.8	39.1	22.7	44.6	47.3	30.1	51.5	45.2	26.5	52.5	44.3
Hi60 x Hi26	25.8	57.8	43.8	29.3	57.9	46.3	24.8	46.8	49.0	28.4	54.5	43.6	27.1	54.3	45.7
Hi61 x Hi62	26.2	48.6	42.3	29.4	51.4	42.2	24.6	34.8	45.4	29.1	44.5	36.7	27.3	44.8	41.6
Hi61 x Hi65	25.1	51.2	39.1	25.2	50.6	40.7	20.3	40.1	44.4	29.6	42.2	33.7	25.1	46.0	39.5
Hi61 x Hi67	24.6	48.6	42.3	29.4	45.9	38.1	22.9	41.1	42.7	26.5	47.9	37.0	25.9	45.9	40.0
Hi61 x Hi26	27.6	47.9	44.1	28.5	51.6	38.7	24.9	40.4	51.0	29.4	46.4	36.9	27.6	46.6	42.7
Hi62 x Hi65	26.7	50.3	38.8	29.9	49.8	44.4	25.9	30.9	46.1	26.2	43.7	36.5	27.2	43.7	41.5
Hi62 x Hi67	27.6	50.8	41.9	32.5	49.6	43.3	26.5	41.8	44.9	30.0	46.8	38.5	29.1	47.3	42.1
Hi62 x Hi26	24.0	49.5	41.9	30.3	49.4	51.8	26.7	39.0	45.3	30.8	45.9	38.3	28.0	45.9	44.3
Hi65 x Hi67	27.4	47.4	35.5	27.3	49.8	39.9	20.7	39.1	45.0	28.8	43.2	32.5	26.1	44.9	38.2
Hi65 x Hi26	24.6	53.1	35.6	28.6	50.0	47.5	23.0	41.9	42.8	29.4	43.6	37.3	26.4	47.2	40.8
Hi67 x Hi26	25.1	53.7	40.8	27.4	53.6	45.4	22.1	46.7	48.7	27.6	47.3	38.1	25.5	50.3	43.2
Hybrid means	26.6	51.6	41.6	29.4	51.1	43.8	25.5	39.1	45.2	28.6	46.1	37.4	27.5	46.9	42.0
Overall mean	26.8	50.5	40.6	28.8	49.9	43.3	25.2	38.7	45.2	28.7	43.8	35.9	27.4	45.7	41.2

Chlorophyll concentrations among hybrids varied greatly across the three growth stages. Based on the means from the four planting dates, highest SPAD at 30 DAP was in Hi53 x Hi60 (30.0) and Hi53 x Hi62 (30.0), while lowest was observed for Hi61 x Hi65 (25.1). At 60 DAP, SPAD ranged from 41.4 (Hi57 x Hi62) to 54.3 (Hi60 x Hi26). Nearing physiologic maturity (90 DAP), SPAD ranged from 36.5 (Hi57 x Hi61) to 45.3 (Hi53 x Hi60).

Comparisons were made between inbred means and their corresponding hybrid array means of their hybrids (Table 6.2). Correlation coefficients were calculated to statistically determine the association between inbred SPAD and their hybrids. For SPAD at 30 DAP, the array means ranged from 26.4 (Hi65) to 28.7 (Hi53). At 60 DAP, means ranged from 44.9 (Hi57) to 51.2 (Hi60) and at 90 DAP, array means ranged from 40.6 (Hi65) to 43.9 (Hi60). At 30 and 60 DAP, higher inbred means per se for Hi53 and Hi60 gave the highest corresponding hybrid array means across the four planting dates. Significant correlations were found between inbred and their hybrid array means for SPAD taken in all the 3 growth stages. Correlation coefficients between inbred means and hybrid array means were higher in 8/04 under low PAR and low temperature across the three growth stages. Correlation coefficients at 60 and 90 DAP were generally high and positive except for the trial in 3/05. Data for the 3/05 planting present many puzzles and are dissimilar from the other three trials. Error variances were high, SPAD values for 30 and 60 DAP were extremely low, and correlations at 60 and 90 DAP were negative. It is suspected that nitrogen fertilization practices contributed to these differences. In 8/04, 84.2% of the variation in hybrid performance for SPAD at 30 DAP was explained by the

Table 6.2. Comparison and correlation between SPAD inbred means and array means within individual and across the four Waimanalo planting dates.

SPAD	Inbreds	Inbred means					Array means				
		7/04	8/04	3/05	5/05	Mean	7/04	8/04	3/05	5/05	Mean
30 DAP	Hi53	32.1	31.4	30.6	33.0	31.8	27.3	30.3	28.2	29.0	28.7
	Hi57	27.6	28.3	24.1	27.1	26.8	27.0	29.0	25.6	28.3	27.5
	Hi60	24.9	26.9	24.0	30.0	26.4	26.8	29.9	26.0	29.2	28.0
	Hi61	26.1	20.6	24.2	26.1	24.2	25.9	28.5	24.8	28.3	26.9
	Hi62	31.2	33.4	24.5	36.0	31.3	26.9	31.2	27.4	29.0	28.6
	Hi65	27.6	20.4	19.7	24.6	23.1	26.0	28.0	23.7	28.0	26.4
	Hi67	23.9	26.4	22.8	25.1	24.6	26.9	29.2	23.5	28.8	27.1
	Hi26	26.3	24.9	25.5	31.8	27.1	25.9	29.1	24.7	28.1	27.0
	Mean	27.5	26.5	24.4	29.2	26.9	26.6	29.4	25.5	28.6	27.5
	r						0.42 *	0.92 **	0.77 **	0.53 *	0.92 **
60 DAP	Hi53	52.6	41.3	33.7	29.1	39.2	51.2	50.7	37.1	44.8	46.0
	Hi57	40.9	43.7	39.3	35.7	39.9	49.7	49.1	37.1	43.7	44.9
	Hi60	54.9	56.2	39.0	45.5	48.9	56.8	54.7	42.7	50.5	51.2
	Hi61	46.0	44.1	34.0	38.1	40.5	50.1	50.5	38.4	45.4	46.1
	Hi62	40.1	37.5	46.6	23.2	36.8	50.1	50.6	35.3	45.3	45.3
	Hi65	46.6	48.1	32.4	32.2	39.8	51.2	50.1	37.6	44.3	45.8
	Hi67	48.8	44.0	38.8	41.7	43.3	51.0	50.4	41.4	46.1	47.3
	Hi26	43.7	50.6	35.1	41.2	42.6	52.6	52.6	42.8	48.4	49.1
	Mean	46.7	45.7	37.4	35.8	41.4	51.6	51.1	39.1	46.1	46.9
	r						0.69 *	0.77 *	-0.23 *	0.67 *	0.91 **
90 DAP	Hi53	46.4	42.4	48.6	26.8	41.0	42.2	45.1	43.6	37.1	42.0
	Hi57	33.5	43.1	43.2	32.8	38.1	41.7	45.1	44.4	35.6	41.7
	Hi60	38.5	39.3	45.0	36.0	39.7	43.8	43.1	47.7	40.9	43.9
	Hi61	38.8	35.0	44.8	29.4	37.0	41.7	40.5	44.9	36.7	41.0
	Hi62	38.4	42.4	47.5	27.5	39.0	41.8	44.1	44.6	37.5	42.0
	Hi65	31.7	42.9	46.5	30.3	37.9	38.8	44.2	44.4	35.2	40.6
	Hi67	32.3	39.0	42.1	29.4	35.7	41.5	41.6	45.1	37.1	41.3
	Hi26	37.0	47.5	43.5	33.9	40.5	41.1	46.9	47.2	38.9	43.5
	Mean	37.1	41.4	45.1	30.8	38.6	41.6	43.8	45.2	37.4	42.0
	r						0.54 *	0.97 **	-0.43 *	0.55 *	0.67 *

inbred line performance, the highest compared to the other planting dates. At 60 DAP, this variation was 58.7% and 93.1% at 90 DAP (Table 6.2).

Analyses of variance for SPAD were determined for the three growth stages in the four Waimanalo trials (Table 6.3). With the exception of the 3/05 planting, highly significant differences occurred among entries and their three components (inbreds, hybrids and inbreds versus hybrids) in all trials.

Coefficients of variation were generally very low for the 12 data sets, except for the 3/05 trial. Replication variations generally were negligible, reflecting the high uniformity of these experimental fields. The 30 DAP were more variable for significance of differences among entries, probably reflecting variations in growth rates and response to side-dressed nitrogen at this early stage.

Data at 60 DAP represent the most critical stage with respect to grain filling. Highly significant differences occurred among inbreds and among hybrids for all trials, and heterosis values were similarly significant with the exception of the unusual 3/05 data set with its very low SPAD readings. The 90 DAP data clearly reflected variations in senescence, e.g., higher error variances, lower SPAD values, greater variability in significance among entries.

In the 5/05 trial the inbreds showed consistent variation for SPAD in 30, 60 ($P<0.01$), and 90 DAP ($P<0.05$) (Table 6.3d). Among hybrids, heterosis and replication variances at 30 DAP were not significant. Heterosis effects were more pronounced at 60 and 90 DAP ($P<0.01$). Variation among replications was evident only at 90 DAP ($P<0.05$).

Table 6.3. Analysis of variance for SPAD readings at 30, 60 and 90 DAP within individual Waimanalo months.

(a) 7/04

Source	df	30 DAP	60 DAP	90 DAP
Entries	35	7.28 **	39.30 **	27.67 **
Inbreds	7	16.52 **	55.35 **	45.32 **
Hybrids	27	4.81 *	25.70 **	14.88 **
I vs H	1	9.20 ns	293.90 **	249.56 **
Reps	1	20.19 **	150.05 **	15.24 ns
Error	35	2.62	6.31	6.00
Total	71			
CV%		6.0%	5.0%	6.0%
Grand mean		26.79	50.50	40.56
$LSD_{0.05}$ Inbreds		3.54	4.73	3.04
$LSD_{0.05}$ Hybrids		3.70	5.96	5.82

(b) 8/04

Source	df	30 DAP	60 DAP	90 DAP
Entries	35	16.82 **	40.85 **	30.67 ns
Inbreds	7	43.05 **	67.22 **	27.31 ns
Hybrids	27	6.82 **	21.97 **	30.07 *
I vs H	1	103.24 **	365.72 **	70.37 *
Reps	1	11.88 *	0.02 ns	124.24 **
Error	35	2.05	6.39	14.76
Total	71			
CV%		5.0%	5.1%	8.9%
Grand mean		28.77	49.89	43.30
$LSD_{0.05}$ Inbreds		4.14	3.98	5.60
$LSD_{0.05}$ Hybrids		2.95	6.18	9.38

(c) 3/05

Source	df	30 DAP	60 DAP	90 DAP
Entries	35	16.45 *	43.12 **	16.86 ns
Inbreds	7	18.38 ns	42.86 **	10.19 ns
Hybrids	27	16.04 ns	43.46 **	19.21 ns
I vs H	1	13.92 ns	35.65 ns	0.08 ns
Reps	1	5.53 ns	3.85 ns	5.41 ns
Error	35	9.09	9.04	10.87
Total	71			
CV%		11.9%	7.8%	7.3%
Grand mean		25.24	38.67	45.21
$LSD_{0.05}$ Inbreds		6.78	7.85	5.98
$LSD_{0.05}$ Hybrids		6.73	6.09	7.74

(d) 5/05

Source	df	30 DAP	60 DAP	90 DAP
Entries	35	11.08 **	82.84 **	37.29 **
Inbreds	7	34.10 **	109.20 **	20.54 *
Hybrids	27	5.34 ns	30.73 **	22.88 **
I vs H	1	4.86 ns	1305.28 **	543.39 **
Reps	1	23.29 ns	12.62 ns	44 47 *
Error	35	3.38	6.11	7.12
Total	71			
CV%		6.4%	5.7%	7.4%
Grand mean		28.71	43.79	35 89
$LSD_{0.05}$ Inbreds		4.02	8.33	6.28
$LSD_{0.05}$ Hybrids		4.25	4.65	5.94

Analysis of variance for chlorophyll concentration was determined using the combined data across the four Waimanalo planting dates (Table 6.4). Months were considered random and entries fixed. For the F-tests, the replications within month mean squares were used as the denominator for months. The entry x month interactions were used as denominator to test the significance of the entries. The pooled error was used to test the significance of the entry x month interactions. Months and replications within months were significant ($P<0.01$). The inbreds showed significant differences ($P<0.01$) for SPAD only at 30 DAP, reflecting the high interaction values of inbreds with the four planting dates (planting dates). Hybrids showed significant differences ($P<0.01$) at all three growth stages. Heterosis for SPAD was not apparent at 30 DAP, but highly significant at 60 DAP. The mean squares for heterosis at 90 DAP was less than that at 60 DAP. Genotype by planting date interactions were significant for the inbreds and hybrids at all growth stages.

In general the interactions of the 8 inbreds with the four planting dates were much greater than interactions involving the 28 hybrids, probably reflecting the increased fitness of single cross hybrids.

Table 6.4. ANOVA of SPAD at 30, 60 and 90 DAP across months.

Source		30 DAP	60 DAP	90 DAP
Months	3	206.75 **	2,247.60 **	1,174.31 **
Reps in Months	4	15.22 **	41.63 **	47.34 **
Entries	35	28.33 **	134.04 **	50.02 **
Inbreds	7	80.34 **	106.08 ns	25.89 ns
Hybrids	27	15.20 **	89.38 **	36.99 **
I vs H	1	18.72 ns	1,535.33 **	570.60 *
Entry x Month	105	7.77 **	24.02 **	20.82 **
Inbreds x M	21	10.57 **	56.19 **	25.83 **
Hybrids x M	81	5.94 *	10.83 *	16.68 **
(I vs H) x M	3	37.50 **	155.07 **	97.60 **
Pooled Error	140	4.29	6.96	9.69
Total	287			
CV %		7.56%	5.77%	7.55%
Mean		27.38	45.71	41.24
$LSD_{0.05}$ Inbreds		4.79	6.50	5.38
$LSD_{0.05}$ Hybrids		4.63	5.75	7.36

6.2.2 Estimation of GCA and SCA effects among planting dates

Estimates for GCA and SCA effects for chlorophyll concentration measured as SPAD were determined among inbreds and hybrids among three growth stages. Measurements were taken at 30, 60 and 90 days after planting (DAP) for each of the four Waimanalo planting dates. Combining abilities for SPAD were determined for the individual and combined planting dates.

Analysis of GCA and SCA effects for SPAD measurements across the three growth stages in 7/04 are shown in Table 6.5a. Highest combining inbreds at 30 DAP inbreds were Hi53 (1.45), Hi62 (0.97), and Hi57 (0.33), while low combining inbreds were Hi61 (-0.79), Hi26 (-0.72), Hi67 (-0.52), Hi65 (-0.37) and Hi60 (-0.34). For the analysis of SCA, SCA effects ranged from -3.28 (Hi53 x Hi61) to 3.08 (Hi57 x Hi67). Hybrids Hi61 x Hi26 (2.36), Hi65 x Hi67 (1.55) and Hi60 x Hi61 (1.42) also had high SCA effects.

At 60 DAP, GCA effects for SPAD were highest for Hi60 (5.30) followed by Hi53 (0.90), Hi26 (0.09) and Hi67 (0.03) (Table 6.5b). Inbreds with low GCA effects included, Hi57 (-2.48), Hi62 (-2.38) and Hi61 (-1.16). Specific combining ability effects were lowest for Hi65 x Hi67 (-2.79) followed by Hi53 x Hi67 (-1.62) and Hi61 x Hi26 (-1.51). Hybrids with highest SCA effects included Hi26 as parent. These include, Hi57 x Hi26 (4.23), Hi67 x Hi26 (3.08), Hi60 x Hi61 (2.80) and Hi65 x Hi26 (2.77). Only one hybrid (Hi61 x Hi26) had a negative SCA (-1.51).

Highest GCA for SPAD at 90 DAP was observed in Hi53 (2.34) which was consistently among the high combiners at 30 and 60 DAP (Table 6.5c). This was

Table 6.5. General (below diagonal) and specific combining ability effects for SPAD taken at 30, 60 and 90 days in the 7/04 trial.

(a) - 30 DAP

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**1.45**	-0.48	-0.64	-3.28	-0.46	-2.16	0.77	1.39
Hi57		**0.33**	0.66	-0.06	-1.56	-0.71	3.08	-1.18
Hi60			**-0.34**	1.42	1.29	0.48	-0.87	0.06
Hi61				**-0.79**	-0.81	-0.50	-0.84	2.36
Hi62					**0.97**	-0.73	0.39	-3.01
Hi65						**-0.37**	1.55	-1.09
Hi67							**-0.52**	-0.44
Hi26								**-0.72**

(b) - 60 DAP

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**0.90**	0.17	0.09	-0.07	0.03	-1.41	-1.62	2.15
Hi57		**-2.48**	1.36	0.08	0.86	1.93	0.63	4.23
Hi60			**5.30**	2.80	2.40	1.54	2.23	1.93
Hi61				**-1.16**	1.63	2.12	-0.72	-1.51
Hi62					**-2.38**	2.42	2.65	1.26
Hi65						**-0.29**	-2.79	2.77
Hi67							**0.03**	3.08
Hi26								**0.09**

(c) - 90 DAP

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**2.34**	2.02	1.42	-1.60	0.80	-2.02	0.98	-3.94
Hi57		**-0.65**	0.03	-2.31	1.65	4.13	2.60	3.40
Hi60			**1.85**	1.32	-1.41	4.06	4.29	1.75
Hi61				**0.42**	0.89	1.11	2.28	3.42
Hi62					**0.41**	0.87	1.91	1.27
Hi65						**-3.03**	-1.00	-1.60
Hi67							**-1.01**	1.52
Hi26								**-0.32**

followed by Hi60 (1.85), Hi61 (0.42) and Hi62 (0.41). The inbreds with the least GCA effects were observed in Hi65 (-3.03), Hi67 (-1.01) and Hi57 (-0.65). Among hybrids with high SCA effects for SPAD at 90 DAP include, Hi60 x Hi67 (4.29), Hi57 x Hi65 (4.13), Hi60 x Hi65 (4.06) and Hi61 x Hi26 (3.42). Lowest SCA effects were observed in Hi53 x Hi26 (-3.94) and Hi53 x Hi65 (-2.02).

General combining ability for chlorophyll concentration in 7/04 varied across the three growth stages (Figure 6.1). Tropical flint inbred Hi53 consistently increased chlorophyll concentration in all three growth stages, while Hi60 a temperate-derived southern dent inbred from Mo17 increased chlorophyll concentration at 60 and 90 DAP only. Inbred Hi65 reduced chlorophyll in all three growth stages while Hi61 reduced chlorophyll at 30 and 60 DAP only.

Combining ability effects for chlorophyll were also determined in 8/04 (Table 6.6). The highest combining inbreds for SPAD at 30 DAP were observed in Hi62 (2.62) and in Hi53 (1.62) (Table 6.6a). Inbred Hi53 was also among the highest combining inbreds at 30 DAP in the 7/04 trial (1.45) (Table 6.5a). Lowest combining inbreds were in Hi65 (-2.23), Hi61 (-1.82) and Hi26 (-0.53). For the SCA analysis, hybrids with the highest SCA effects were Hi60 x Hi65 (3.62), Hi61 x Hi67 (2.60), and Hi53 x Hi61 (2.5). Lowest SCA effects were in two hybrids with Hi53 as one of the parents. These were Hi53 x Hi57 (-1.69), Hi53 x Hi65 (-1.10) and in Hi67 x Hi26 (-0.70).

Magnitudes of GCA effects at 60 DAP ranged from -1.98 (Hi62) to 4.61 (Hi60) (Table 6.6b). Inbred Hi60 was consistently a high combiner at 60 DAP as it was in 7/04. General combining ability effect for Hi62 was the lowest at 60 DAP (-1.98) as opposed

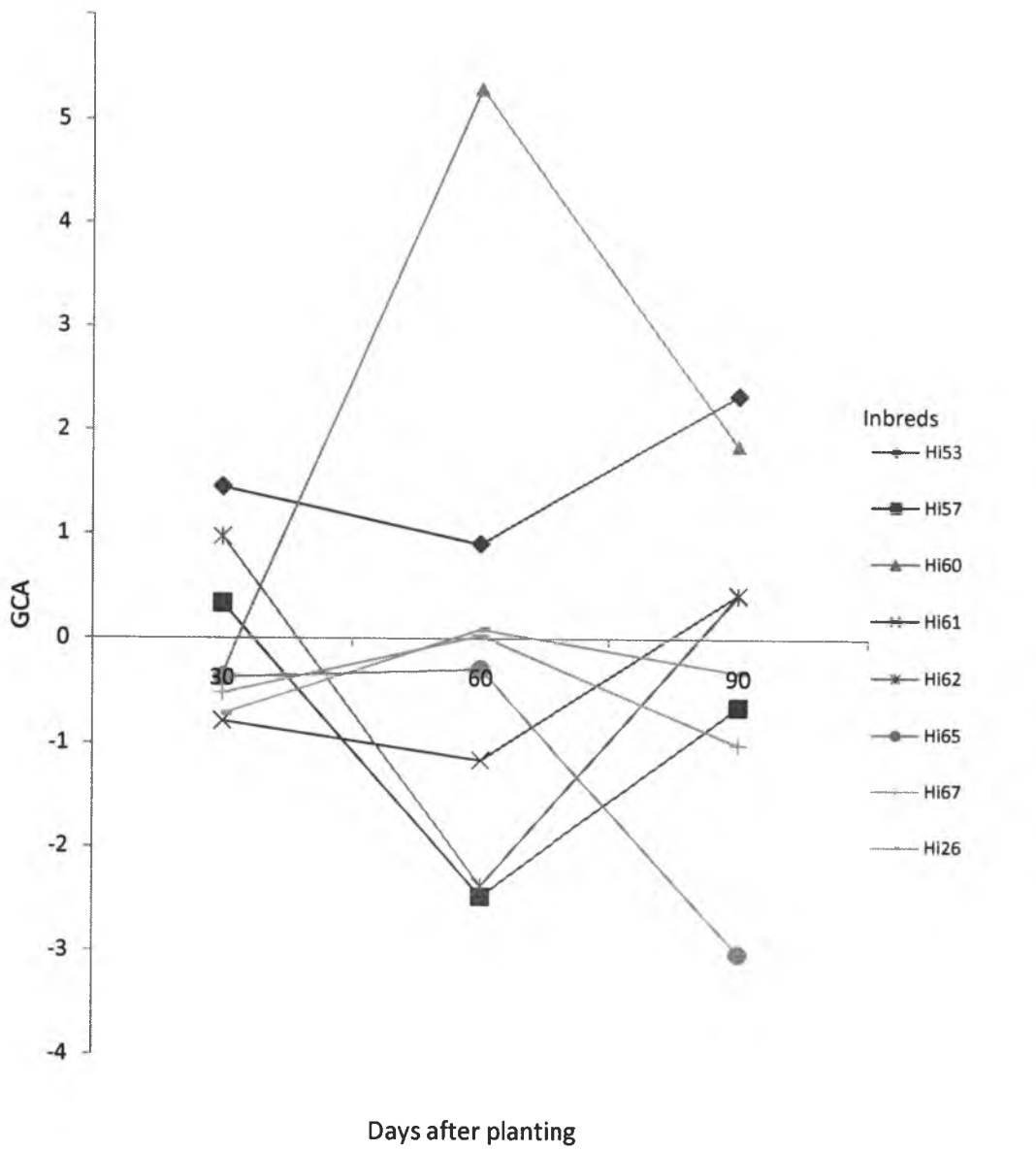

Figure 6.1. General combining ability x growth stage interaction for SPAD in 7/04.

its GCA observed at 30 DAP (2.62) (Table 6.6a). Other high GCA inbreds include, Hi26 (2.06) and Hi65 (-0.21). Two hybrids with Hi53 as one of its parents were among those with high SCA effects. These were Hi53 x Hi61 (5.81) and Hi53 x Hi62 (5.79). The SCA effect of Hi53 x Hi61 (2.50) was also the highest for SPAD at 30 DAP (Table 6.6a). Other hybrids with higher SCA effects include Hi57 x Hi67 (5.52), Hi61 x Hi61 (4.18) and Hi53 x Hi26 (3.71).

For SPAD at 90 DAP, high combining inbreds were Hi26 (3.39), Hi57 (1.22) and Hi53 (1.10) (Table 6.6c). The GCA effects for Hi53 and Hi26 were consistently the highest among the earlier growth stages (Table 6.6a and 6.6b). Lowest GCA effects were observed in Hi61 (-3.62), Hi67 (-2.01) and Hi60 (-0.96). Specific combining ability effects were consistently high for Hi53 x Hi61 which was comparable to the SCA effect for SPAD at 60 DAP (5.81) (Table 6.6b). This hybrid also had a high SCA effect (2.50) at 30 DAP. Other hybrids with high magnitudes of SCA effects at 90 DAP include, Hi57 x Hi60 (4.91), Hi62 x Hi26 (4.71) and Hi57 x Hi67 (3.82). Lowest SCA effects were Hi61 x Hi26 (-4.33), Hi57 x Hi62 (-3.21) and in Hi53 x Hi67 (-2.92).

Magnitudes of GCA effects were inconsistent across the three growth stages for the trial planted in 8/4 under the lowest PAR and temperature (Figure 6.2). Inbred Hi60 increased chlorophyll concentration (GCA > 0.00) at earlier growth stages (30 and 60 DAP), while inbred Hi26 increased chlorophyll concentration at later growth stages (60 and 90 DAP). Inbreds Hi61 and Hi67 reduced chlorophyll concentration (GCA < 0.00) in all the three growth stages.

Table 6.6. General (below diagonal) and specific combining ability effects for SPAD taken at 30, 60 and 90 days in the 8/04 2004 trial.

(a) - 30 DAP

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**1.62**	-1.69	1.27	2.50	-0.23	-1.10	0.62	-0.14
Hi57		**0.04**	-0.37	1.05	-0.49	0.54	0.27	1.80
Hi60			**0.45**	0.59	0.65	3.62	-0.76	0.57
Hi61				**-1.82**	-0.21	0.51	2.60	2.10
Hi62					**2.62**	0.79	1.20	-0.54
Hi65						**-2.23**	0.91	2.57
Hi67							**-0.14**	-0.70
Hi26								**-0.53**

(b) - 60 DAP

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**-1.12**	-0.91	0.80	5.81	5.79	0.03	-2.59	3.71
Hi57		**-1.81**	-0.50	-1.84	1.01	0.60	5.52	1.22
Hi60			**4.61**	1.02	1.89	-0.83	2.12	1.35
Hi61				**-0.72**	4.18	1.63	-2.48	0.39
Hi62					**-1.98**	2.09	2.49	-0.55
Hi65						**-0.21**	0.99	-1.71
Hi67							**-0.83**	2.50
Hi26								**2.06**

(c) - 90 DAP

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**1.10**	-1.23	1.64	5.92	-1.08	1.00	-2.92	2.87
Hi57		**1.22**	4.91	-2.07	-3.21	2.87	3.82	0.27
Hi60			**-0.96**	-0.44	-1.13	-0.17	-1.26	0.55
Hi61				**-3.62**	2.17	0.53	0.39	-4.33
Hi62					**0.36**	0.18	1.65	4.71
Hi65						**0.52**	-1.92	0.33
Hi67							**-2.01**	0.76
Hi26								**3.39**

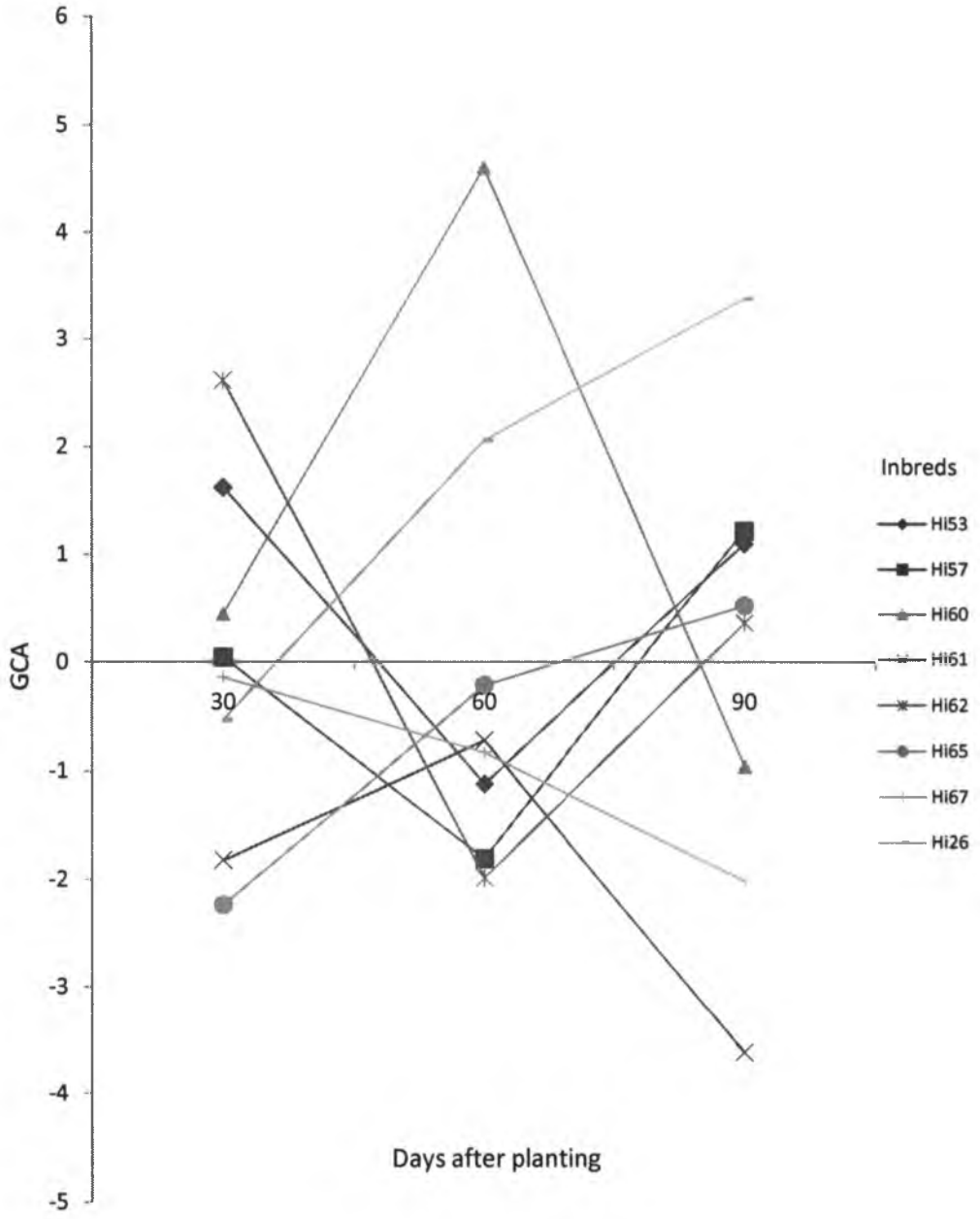

Figure 6.2. General combining ability x growth stage interaction for SPAD in 8/04.

General combining ability effects was highest for Hi53 (3.10) in 3/05 for SPAD at 30 DAP (Table 6.7a) as it was for the trials planted in 7/04 (Table 6.5a) and in 8/04 (Table 6.6a). Other high GCA inbreds include Hi62 (1.38), which was consistently a high combiner in 7/04 and 8/04, Hi60 (0.28) and Hi57 (0.02). Lowest GCA inbreds were Hi65 (-1.38) and Hi60 (0.28). Specific combining ability effects ranged from -2.34 (Hi57 x Hi26) to 3.74 (Hi60 x Hi61). Other hybrids with high SCA effects were, Hi57 x Hi62 (3.49), Hi53 x Hi65 (2.53) and Hi60 x Hi62 (2.10).

Inbred Hi60 had the highest GCA effect for SPAD at 60 DAP (Table 6.7b) as it also was for the trials planted in 7/04 (Table 6.5b) and in 8/04 (Table 6.6b). A decrease in GCA effects for Hi62 at 60 DAP were also observed at this growth stage, from 1.38 to -0.76 which were observed previously in the trials planted in 7/04 (from 0.97 to -2.38) and in 8/04 (from 2.62 to -1.98). Other inbreds that were observed to have high GCA effects were Hi26 (2.15) and Hi67 (1.96). Lowest GCA inbreds at 60 DAP were Hi53 (-2.07), Hi65 (-2.02) and Hi61 (-1.15). For SCA analysis, SCA effects were lowest for Hi60 x Hi62 (-5.22) and highest for Hi60 x Hi61 (5.78). Other hybrids with comparable high SCA effects include Hi61 x Hi65 (4.54) and Hi53 x Hi26 (4.53).

At 90 DAP, GCA effects were highest for Hi60 (1.69) followed by Hi26 (1.04) and Hi62 (0.02) (Table 6.7c). Inbreds with low GCA include Hi67 (-0.69), Hi53 (-0.47), Hi61 (-0.29) and Hi65 (-0.29). Specific combining ability effects among hybrids ranged from -6.35 (Hi57 x Hi61) to 4.99 (Hi61 x Hi26). Other high SCA hybrids that were indentified include Hi53 x Hi60 (3.31) and Hi67 x Hi26 (3.09).

Table 6.7. General (below diagonal) and specific combining ability effects for SPAD taken at 30, 60 and 90 days in the 3/05 trial.

(a) - 30 DAP

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**3.10**	-0.38	1.20	-1.57	-0.64	2.53	-0.05	0.69
Hi57		**0.02**	-0.98	1.01	3.49	2.06	-0.51	-2.34
Hi60			**0.28**	3.74	2.10	-1.07	-1.10	-0.37
Hi61				**-0.55**	-1.52	-2.20	-0.06	0.54
Hi62					**1.38**	1.51	1.56	0.46
Hi65						**-2.18**	-0.66	0.28
Hi67							**-1.69**	-1.14
Hi26								**-0.35**

(b) - 60 DAP

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**-2.07**	2.26	1.59	-4.32	-3.03	0.71	0.01	4.53
Hi57		**-1.00**	1.24	-1.51	-4.64	-2.65	-1.48	1.45
Hi60			**2.89**	5.78	-5.22	3.26	1.06	3.12
Hi61				**-1.15**	-1.99	4.54	1.64	0.70
Hi62					**-0.76**	-5.02	1.97	-1.05
Hi65						**-2.02**	0.49	3.13
Hi67							**1.96**	3.95
Hi26								**2.15**

(c) - 90 DAP

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**-0.47**	-2.43	3.31	-0.24	-2.38	-4.64	-2.35	0.10
Hi57		**-1.00**	1.99	-6.35	-0.92	2.98	2.17	2.58
Hi60			**1.69**	2.50	-2.22	-0.62	1.05	1.07
Hi61				**-0.29**	0.47	-0.20	-1.54	4.99
Hi62					**0.02**	1.14	0.36	-1.00
Hi65						**-0.29**	0.78	-3.18
Hi67							**-0.69**	3.09
Hi26								**1.04**

Inbred Hi60 a temperate inbred from Mo17 increased chlorophyll concentration in all three growth stages for the trial in 3/05 (Figure 6.3). The ability of inbred Hi60 to increase chlorophyll concentration at later stages of growth was also evident in the previous trials in 7/04 and 8/04. Inbreds Hi51, Hi57 and Hi61 reduced chlorophyll concentration in all growth stages. Inbreds Hi53 and Hi62 reduced chlorophyll concentration at later stages of growth (60 and 90 DAP).

Combining ability effects for SPAD at 30, 60 and 90 DAP were also determined for the trial planted in 5/05. Inbreds with high GCA effects for chlorophyll concentration at 30 DAP were Hi53 (1.04), Hi62 (1.62) and Hi60 (0.57) (Table 6.8a). High GCA effects at 30 DAP for both inbreds were also observed in previous trials planted in 7/04 and 8/04, and 3/05. Inbreds with low GCA effects at this growth stage include, Hi65 (-1.35), Hi61 (-0.84), Hi67 (-0.67), and Hi57 (-0.61). Magnitudes of SCA effects for SPAD at 30 DAP in 5/05 ranged from -3.73 (Hi53 x Hi26) to 3.05 (Hi61 x Hi65).

Similar to the trials in 2004 and for the trial in 3/05, GCA effects of inbreds Hi53 and Hi62 decreased at 60 DAP (Table 6.8b). General combining ability effects for both inbreds were -2.25 (Hi53) and -3.07 (Hi62). Highest GCA inbred was Hi60 (5.06) which was consistently the highest combining for the trials planted previously in 2004 and in 3/05. For SCA analysis, SCA effects ranged from -1.81 (Hi57 x Hi61) to 6.40 (Hi53 x Hi26). Other hybrids that had prominently high SCA effects include Hi60 x Hi62 (6.39), Hi57 x Hi60 (5.50), Hi57 x Hi65 (4.96) and Hi62 x Hi65 (4.96).

For SPAD at 90 DAP, the highest combining inbreds were found for Hi60 (3.52) and Hi26 (1.70) (Table 6.8c). Inbred Hi60 had consistently high GCA effects for SPAD

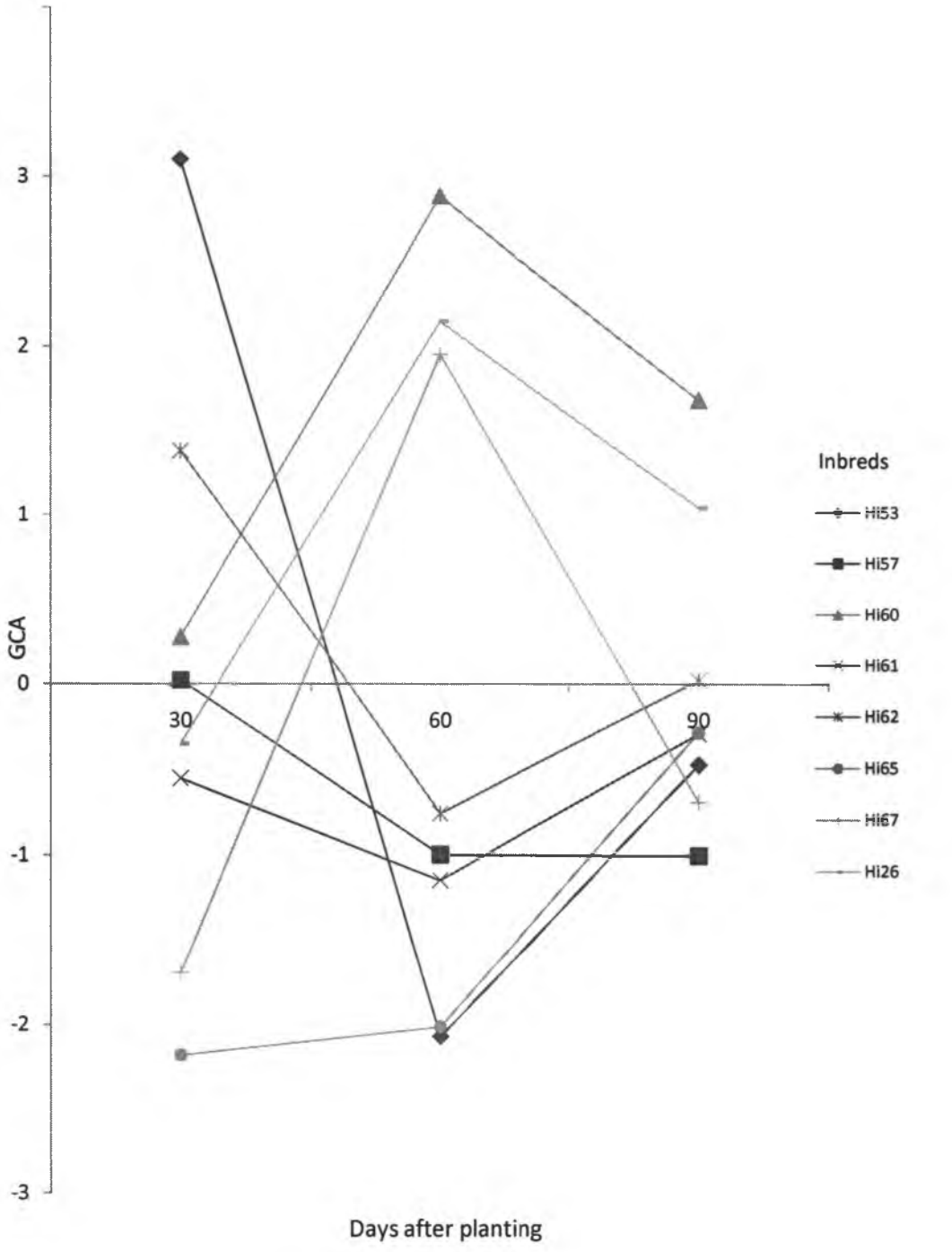

Figure 6.3. General combining ability x growth stage interaction for SPAD in 3/05.

Table 6.8. General (below diagonal) and specific combining ability effects for SPAD taken at 30, 60 and 90 days in the 5/05 trial.

(a) - 30 DAP

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**1.04**	1.82	0.64	-1.24	-1.91	-0.22	0.30	-3.73
Hi57		**-0.61**	1.99	-0.39	-0.03	-1.10	1.67	-3.11
Hi60			**0.57**	0.31	-3.39	-0.05	1.45	-1.13
Hi61				**-0.84**	-0.40	3.05	-0.68	1.26
Hi62					**1.62**	-2.81	0.29	0.25
Hi65						**-1.35**	2.13	1.82
Hi67							**-0.67**	-0.67
Hi26								**0.23**

(b) - 60 DAP

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**-2.25**	1.46	-0.70	3.76	6.02	1.94	1.61	6.40
Hi57		**-1.69**	0.09	-1.81	0.56	4.96	-1.32	5.50
Hi60			**5.06**	2.64	6.39	4.00	1.40	2.94
Hi61				**-0.0038**	3.75	0.36	2.86	-0.10
Hi62					**-3.07**	4.96	4.84	2.47
Hi65						**-1.96**	0.09	-0.94
Hi67							**1.23**	-0.39
Hi26								**2.68**

(c) - 90 DAP

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**-0.97**	3.03	1.61	1.62	3.52	3.49	-1.20	2.32
Hi57		**-0.85**	-1.38	-2.91	0.62	0.64	0.46	2.37
Hi60			**3.52**	6.94	0.57	-2.62	6.24	2.47
Hi61				**-0.71**	2.02	0.19	2.24	0.01
Hi62					**-0.57**	2.85	3.62	1.28
Hi65						**-1.65**	-1.29	1.39
Hi67							**-0.48**	1.01
Hi26								**1.70**

at 90 DAP in previous trials (7/04 and 3/05). Low combining inbreds for SPAD at 90 DAP were Hi65 (-1.65), Hi53 (-0.97), Hi57 (-0.85), Hi61 (-0.71) and Hi62 (-0.57). For the SCA analysis, highest SCA effects were observed in Hi60 x Hi67 (6.24), Hi62 x Hi67 (3.62), Hi53 x Hi62 (3.52) and Hi53 x Hi65 (3.49). The hybrid with the lowest SCA was Hi57 x Hi61 (-2.91).

Inbreds Hi60 and Hi26 increased chlorophyll concentration in all the three stages of growth in the summer trial (5/05) (Figure 6.4). Inbred Hi60 was bred from Mo17 which was bred to adapt to longer days (>16 hr light periods), and early maturing to avoid frost in temperate regions. Inbreds Hi57 and Hi65 reduced chlorophyll concentration in all three growth stages. Inbred Hi61 a tropical highland dent had no change in chlorophyll concentration.

6.2.3 Analysis of GCA and SCA effects across planting dates

The analysis for GCA and SCA effects was performed for combined chlorophyll data in the four planting dates. For SPAD measurements taken at 30 DAP, inbreds Hi53 (1.8), Hi62 (1.65) and Hi60 (0.24) were among the highest combiners (Table 6.9a). Inbreds Hi65 (-1.54), Hi61 (-1.00), Hi67 (-0.76), Hi26 (-0.34) and Hi57 (-0.05) had the lowest GCA effects at 30 DAP. For the SCA analysis, magnitudes of SCA effects among hybrids ranged from -1.21 (Hi57 x Hi26) to 1.52 (Hi60 x Hi61). Higher magnitudes of SCA effects were also observed in hybrids Hi57 x Hi67 (1.13), Hi60 x Hi61 (1.52) and Hi65 x Hi67 (0.98).

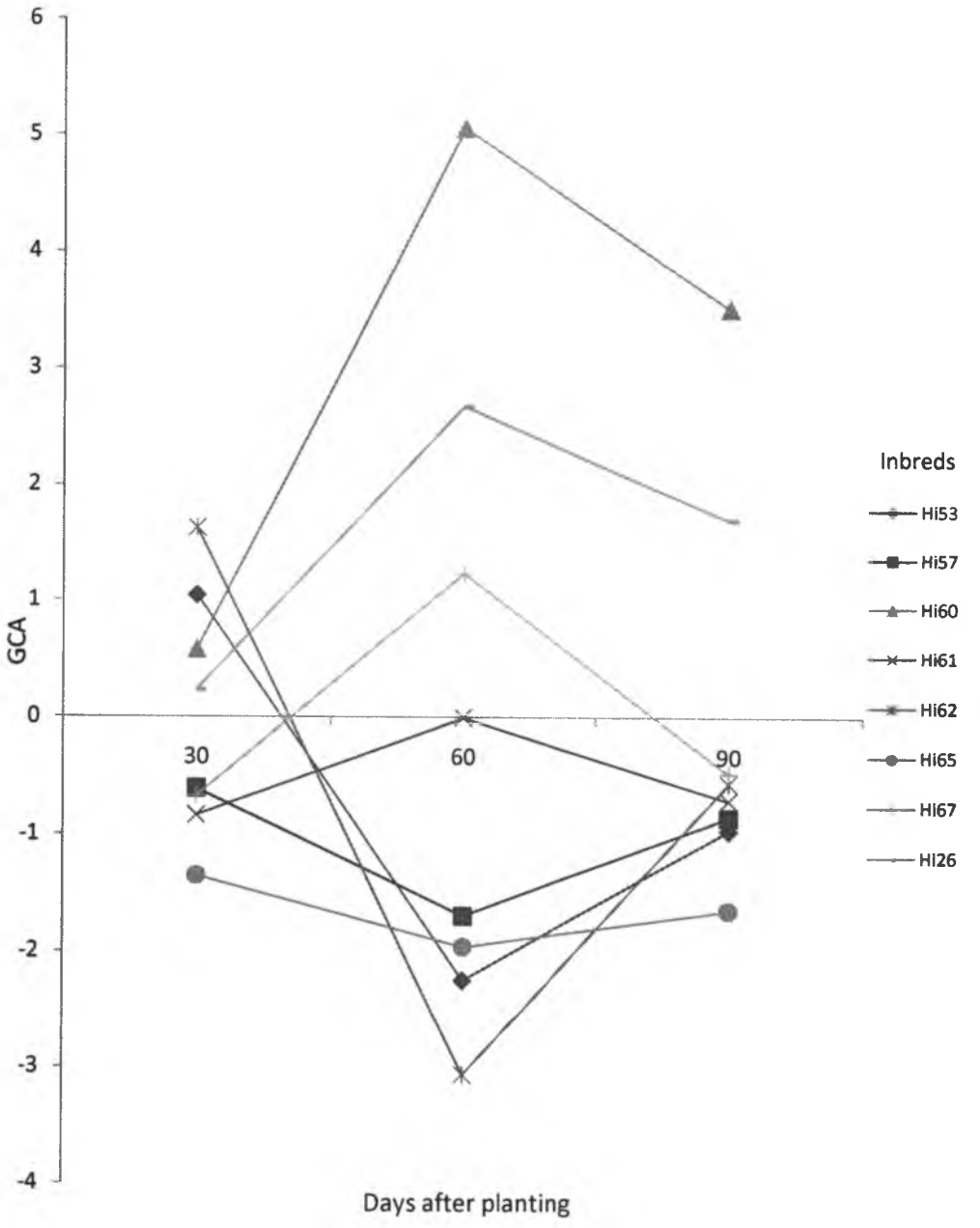

Figure 6.4. General combining ability x growth stage interaction for SPAD in 5/05.

Table 6.9. General (below diagonal) and specific combining ability effects for SPAD taken at 30, 60 and 90 days after planting across seasons.

(a) 30 DAP

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**1.80**	-0.18	0.61	-0.90	-0.81	-0.24	0.41	-0.45
Hi57		**-0.05**	0.32	0.40	0.35	0.19	1.13	-1.21
Hi60			**0.24**	1.52	0.16	0.75	-0.32	-0.22
Hi61				**-1.00**	-0.73	0.21	0.26	1.56
Hi62					**1.65**	-0.31	0.86	-0.71
Hi65						**-1.54**	0.98	0.89
Hi67							**-0.76**	-0.74
Hi26								**-0.34**

(b) 60 DAP

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**-1.13**	0.75	0.45	1.29	2.20	0.32	-0.65	**4.20**
Hi57		**-1.75**	0.55	-1.27	-0.55	1.21	0.84	3.10
Hi60			**4.46**	3.06	1.36	1.99	1.70	2.34
Hi61				**-0.76**	1.89	2.16	0.32	-0.13
Hi62					**-2.05**	1.11	2.99	0.53
Hi65						**-1.12**	-0.30	0.81
Hi67							**0.60**	2.28
Hi26								**1.75**

(c) - 90 DAP

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**0.50**	0.35	2.00	1.42	0.21	-0.54	-1.37	0.34
Hi57		**-0.32**	1.39	-3.41	-0.47	2.66	2.26	2.15
Hi60			**1.53**	2.58	-1.05	0.16	2.58	1.46
Hi61				**-1.05**	1.39	0.41	0.85	1.02
Hi62					**0.06**	1.26	1.89	1.56
Hi65						**-1.11**	-0.86	-0.77
Hi67							**-1.05**	1.59
Hi26								**1.45**

Similar to the analysis of GCA effects performed in the individual planting dates, Hi60 gave the highest GCA (4.46) for SPAD measurements taken at 60 DAP (Table 6.9b). A decline in GCA effects for Hi53 (from 1.8 to -1.13) and Hi62 (from 1.65 to -2.05) was also observed between the two inbreds, consistent for the trials planted among the four Waimanalo planting dates. Lowest GCA inbreds following Hi62 were Hi57 (-1.75), Hi65 (-1.12) and Hi61 (-0.76). The magnitudes of SCA effects among hybrids were highest for Hi53 x Hi26 (4.20), Hi57 x Hi26 (3.10) and Hi60 x Hi61 (3.06). Lastly the hybrids with the lowest SCA effects were Hi57 x Hi61 (-1.27), Hi53 x Hi67 (-0.65) and Hi57 x Hi65 (-0.55).

General combining ability effects for SPAD taken at 90 DAP were highest for Hi60 (1.53) followed by Hi26 (1.45) and Hi53 (0.50) (Table 6.9c). The high magnitudes of GCA effects for Hi60 and Hi53 for this growth stage were consistent for trials planted in 2004 and in 2005. Inbreds that had the lowest GCA effects were Hi65 (-1.11) and Hi57 (-0.32). Inbreds Hi61 and Hi67 had the same GCA effects (-1.05). Among hybrids, SCA effects ranged from -3.41 (Hi57 x Hi61) to 2.58 (Hi60 x Hi61 and Hi60 x Hi67).

Inbred Hi60 increased chlorophyll concentration in all three growth stages (Figure 6.5) consistent for the trials in 7/04, 3/05 and 5/05. Inbred Hi26 increased chlorophyll at 60 and 90 DAP. Inbreds Hi65 and Hi61 reduced chlorophyll concentration in all growth stages.

Summarizing, it is concluded that 60 DAP data for SPAD must effectively relate to grain filling phenomena. At this time the high GCA values of Hi60 (Mo17) and Hi26

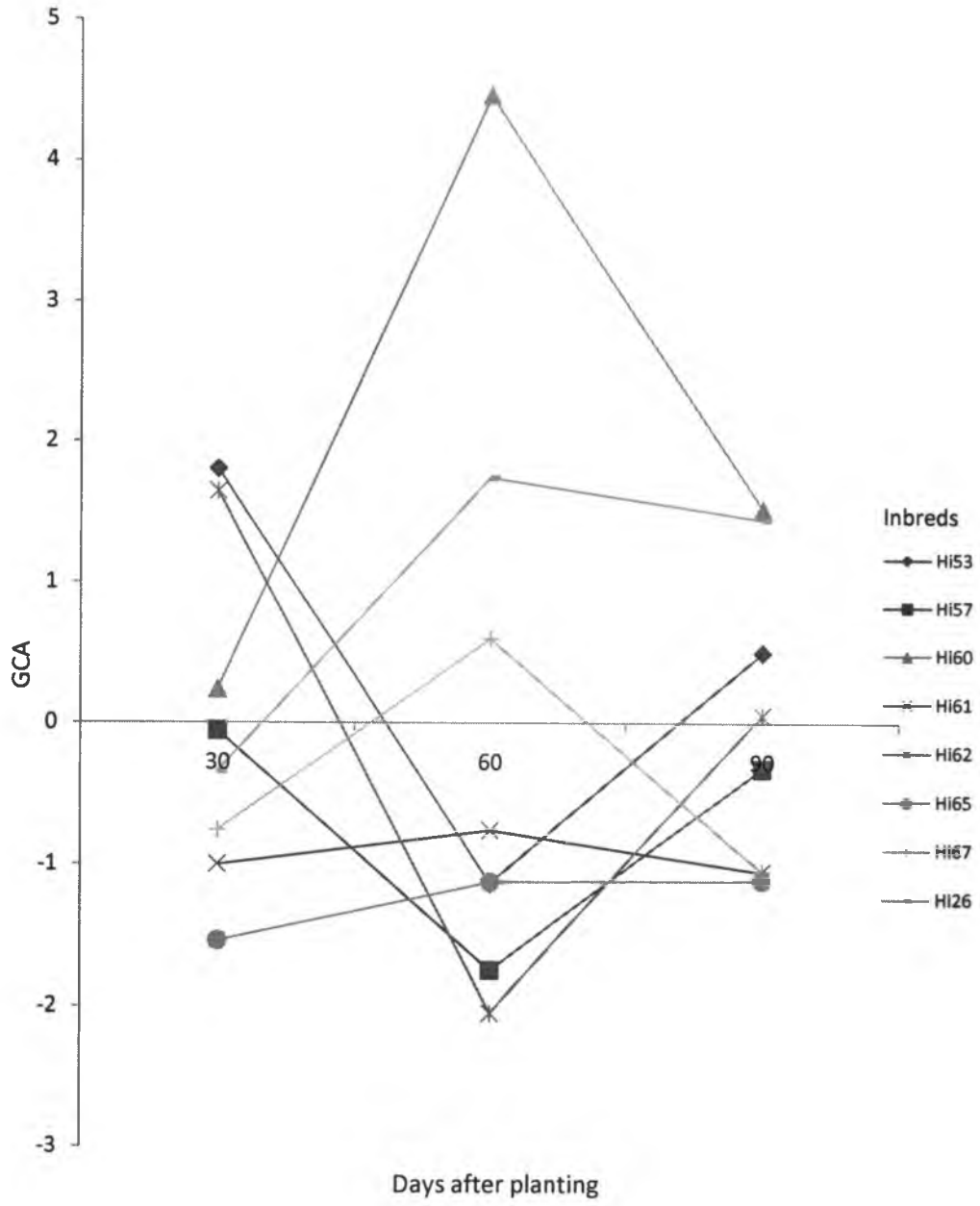

Figure 6.5. General combining ability x growth stage interaction for SPAD across Waimanalo months.

are outstanding, and maybe of significance in relation to grain filling rates of their hybrids (cf. Table 2.4, Chapter 2).

6.2.4 Analysis of variance for GCA and SCA effects

Analysis of variance for both GCA and SCA effects was performed among the four Waimanalo planting dates and combined data. Mean squares for GCA and SCA as well as the ratios of GCA to SCA to estimate their relative contributions to the genetic control of chlorophyll concentration were determined. Both GCA and SCA effects were significant for SPAD taken at 30, 60 and 90 DAP in all four Waimanalo planting dates (Table 6.10). For the trials planted in 7/04 and in 8/04, GCA effects were highly significant ($P<0.01$) for SPAD at 30, 60 and 90 DAP. Specific combining ability effects were also significant at 30 DAP ($P<0.05$), 60 DAP ($P<0.01$) and 90 (DAP) for the trials planted in 7/04 ($P<0.05$) and in 8/04 in all growth stages ($P<0.01$). Ratios of GCA to SCA mean squares indicated that GCA is predominant than SCA in the genetic control of chlorophyll concentration in all growth stages for the trials planted in 7/04 and in 8/04 (Table 6.10). Ratios were 1.73, 4.52 and 2.00 for 30, 60 and 90 DAP, respectively for the trial planted in 7/04. For the trial in 8/04, ratios were 4.70, 2.77 and 4.45, for SPAD at 30, 60 and 90 DAP, respectively, suggesting the predominance GCA over SCA for SPAD in all growth stages.

For the trials planted in 3/05 and 5/05, both GCA and SCA were highly significant in all stages of growth ($P<0.01$) (Table 6.10). For the trial planted in 3/05, greater ratios of GCA to SCA mean squares for SPAD at 30 (6.15) and 60 DAP (1.69)

Table 6.10. Analysis of variance for general and specific combining ability effects among the four Waimanalo planting dates.

		7/04		
Source	df	30 DAP	60 DAP	90 DAP
GCA	7	6.868 **	60.205 **	28.524 **
SCA	20	3.963 *	13.312 **	14.228 **
Error	35	2.108	2.108	2.108
Ratio				
2GCA/(2GCA+SCA)		0.78	0.90	0.80
GCA:SCA		1.73	4.52	2.00

		8/04		
Source	df	30 DAP	60 DAP	90 DAP
GCA	7	26.150 **	50.289 **	46.670 **
SCA	20	5.565 **	18.139 **	10.498 **
Error	35	2.108	2.108	2.108
Ratio				
2GCA/(2GCA+SCA)		0.90	0.85	0.90
GCA:SCA		4.70	2.77	4.45

		3/05		
Source	df	30 DAP	60 DAP	90 DAP
GCA	7	28.071 **	40.041 **	8.314 **
SCA	20	4.567 **	23.716 **	11.840 **
Error	35	2.108	2.108	2.108
Ratio				
2GCA/(2GCA+SCA)		0.92	0.77	0.58
GCA:SCA		6.15	1.69	0.70

		5/05		
Source	df	30 DAP	60 DAP	90 DAP
GCA	7	10.644 **	79.220 **	29.637 **
SCA	20	5.969 **	44.756 **	22.252 **
Error	35	2.108	2.108	2.108
Ratio				
2GCA/(2GCA+SCA)		0.78	0.78	0.73
GCA:SCA		1.78	1.77	1.33

also suggest the importance of GCA over SCA in the genetic control of chlorophyll concentration. However in this planting date, SCA effects were more prominent for SPAD taken at 90 DAP as evidenced by greater SCA mean square and a GCA to SCA ratio of 0.70. Lastly, ratios of GCA to SCA mean squares for the trial planted in 5/05 also suggest that GCA is more prominent than SCA in the genetic control of chlorophyll concentration in all growth stages.

In the analysis of variance for the combined data across the four Waimanalo planting dates, GCA effects only were found to be significant ($P<0.01$) for SPAD measurements taken at 30 DAP (Table 6.11). Variation for both GCA ($P<0.01$) and SCA effects ($P<0.01$) were both significant at 60 DAP. Finally at 90 DAP, only the variations in SCA effects ($P<0.01$) were found to be significant.

Combining ability by planting date interactions were also determined for SPAD measurements in the three growth stages (Table 6.11). Highly significant GCA x M interactions ($P<0.01$) were consistent among the three growth stages. Specific combining ability x month interactions were also significant at 30 DAP ($P<0.05$), 60 DAP ($P<0.01$) and 90 DAP.

Greater mean squares for GCA and higher ratios of GCA to SCA effects for the combined data indicate that GCA is more important than SCA in the genetic control of chlorophyll concentration. The GCA to SCA ratios were 17.36 (30 DAP), 5.39 (60 DAP) and 2.41 (90 DAP), an apparently meaningful trend.

Table 6.11. Analysis of variance for combining ability effects for SPAD at 30, 60 and 90 DAP across Waimanalo months.

Source	df	Mean squares		
		30 DAP	60 DAP	90 DAP
GCA	7	57.55 **	192.42 **	47.04 ns
SCA	28	3.32 ns	35.67 **	19.50 **
GCA x M	21	4.73 **	12.45 **	22.04 **
SCA x M	84	3.67 *	11.90 **	7.50 *
Pooled error	140	2.14	3.48	4.84
Ratio				
2GCA/(2GCA+SCA)		0.97	0.92	0.83
GCA:SCA		17.36	5.39	2.41

6.3 Discussions

Chlorophyll concentrations in this study varied greatly among the three growth stages, and among the four Waimanalo planting dates. Mean chlorophyll concentrations measured as SPAD were generally lowest at 30 DAP (early vegetative, soon after sidedress fertilization 5 – 8 leaf stages) and highest at 60 DAP (tassel, silking stages), decreasing at the 90 DAP among inbreds and hybrids. Chlorophyll readings among inbreds and hybrids among the three growth stages were slightly lower in the summer compared to the readings in the autumn planting in 8/04. Average light in the summer plantings was 50% more (42 moles m^{-2} day^{-1}) as opposed to the trial planted in 8/04 (18 moles m^{-2} day^{-1}). In plants, excessive light may cause photoinhibition of photosynthesis (for review see Long et al. 1994). High temperatures also enhance photoinhibition of photosynthesis (Bongi and Long, 1987). It is possible therefore that because of the higher light levels and warmer temperatures in the summer plantings as opposed to the autumn planting in Waimanalo, photoinhibition may have occurred resulting to slightly lower chlorophyll readings in the summer trials compared to the trial in 8/04.

Weather records showed a fairly high amount of rainfall in March 2005 (4.57 in) indicating more cloud cover compared to May 2005 (2.63 in) that may have resulted to higher error variances observed in the trial planted in March 16, 2005 (3/05). Low incident light during the winter months at the windward areas in Oahu such as in Waimanalo result to shorter plants and 50% reduction in yields relative to the summer (Brewbaker, 2003).

Chlorophyll concentrations are also influenced by other factors. Peterson et al. (1993) and Turner and Jund (1994) reported that SPAD values are affected by seasonal differences in radiation, plant density, varietal groups, nutrient status and biotic and abiotic stresses that induce leaf discoloration. Leaf CO_2 exchange rates (CER) were highest during the vegetative stage compared to grain filling stage of growth in maize from a complete diallel planted in two different years at Ames, Iowa (Crosbie et al., 1978). Nourse et al. (1999) reported significant genetic differences, as measured by SPAD at 30 DAP in response to iron deficiency in calcareous soils. A major QTL was mapped on chromosome 4.

Significant correlations occurred between inbred SPAD means and their corresponding hybrid array means. Significant heterosis effects for SPAD were found in some Waimanalo seasons. For the combined analysis in this study, heterosis was significant for SPAD at 60, which was largest in magnitude based on the mean squares, followed by SPAD at 90 DAP. Heterosis effects were not significant at 30 DAP. Significant heterosis effects for chlorophyll concentration in the vegetative and grain filling stages of growth in maize were also reported in the previous work of Crosbie et al., (1978), which showed greater mean squares for heterosis (inbreds versus crosses) during grain filling compared to the vegetative stage of growth. It is obvious that SPAD readings at 60 DAP were the most important and reliable, as characterized by least coefficients of variation for most trials. Variations in senescence at 90 DAP resulted to higher error variances, greater variability or significance among entries.

Inbred Hi60, a temperate dent from Mo17, increased chlorophyll concentration in all three growth stages consistent for the trials summer in 7/04, 3/05 and 5/05 under high PAR and temperature. Inbred Hi26 also increased chlorophyll at 60 and 90 DAP. Inbreds Hi65 and Hi61 reduced chlorophyll concentration in all growth stages.

Richards (2000) reported that a genetic increase in the rate of photosynthesis per unit leaf area has not yet been achieved, mainly because of increased use and dependence on nitrogen fertilizers. This study in Waimanalo has shown that it is possible to increase chlorophyll concentration using breeding methods that take advantage of additive variation such as recurrent selection methods. In this study, additive gene effects were prevalent for chlorophyll concentrations among the three growth stages, among seasons, and the combined analysis as shown by higher ratios of GCA to SCA mean squares (GCA: SCA ratio of 5.4 at 60 DAP overall). The importance of additive gene effects in this study also support the findings of Crosbie et al. (1978) who found higher ratios of GCA to SCA for photosynthesis measured as carbon dioxide exchange rates during the vegetative and grain filling stages of growth.

Both GCA and SCA x M were significant suggesting that the magnitude of additive and non-additive gene effects varied across seasons. General combining ability x season interactions were generally larger than SCA x M in all growth stages. Crosbie et al. (1978) also reported larger GCA x M ($P<0.01$) mean squares than SCA x M in a diallel among 8 inbreds.

With the consistency of these effects it may be possible to do selections for increased chlorophyll concentration in any of the three growth stages using a SPAD

meter. The use of a SPAD meter allows rapid determination of chlorophyll concentration without having to resort to destructive sampling methods. However selection for chlorophyll concentration per se may not significantly improve yield. In this study, chlorophyll concentrations in all the three growth stages were not significantly correlated with kernel weights and plant yield. Other traits, such as leaf area, leaf number and "stay green" (leaf area duration) should also be studied in relation to improve photosynthetic efficiency.

CHAPTER 7
DIALLEL ANALYSIS OF AGRONOMIC TRAITS IN MAIZE

7.1 Introduction

This study was conducted to (1) determine genetic variation and genotype by month interaction for days to mid-anthesis, days to mid-silk, plant height and ear height, kernel number and kernel row number, kernel weight and plant yield and kernel density, (2) to determine general combining ability (GCA) and specific combining ability effects (SCA) for the aforementioned traits and (3) to determine GCA and SCA x month interactions. Information on the genetic variation, combining ability effects, and genotype x month interactions will influence the appropriate breeding strategies for improvement of these traits. Eight elite inbreds representing diverse heterotic groups that had been released previously (Brewbaker and Josue, 2007) were crossed in a diallel (Chapter 2). The 28 hybrids and the eight inbreds were planted in four Waimanalo months, July 2004 (7/04), August 2004 (8/04), March 2005 (3/05), and May 2005 (5/05) in a randomized complete block with two replications using the fixed effects model. The inbreds were randomized separately to avoid competition effects from the hybrids. Measurements of the aforementioned traits and statistical analysis are described previously in Chapter 2. A total of ten plants per plot were measured for ear height and plant height while five ears per plot were measured for kernel number and kernel row number, kernel weight and plant yield and kernel density. Kernel density was determined using the water displacement method from a sample of 500 kernels from 5 ears.

7.2 Results

7.2.1 Mean performance and analysis of variance

7.2.1.1 Days to mid-anthesis and days to mid-silk

Mean days to mid-anthesis among inbreds and hybrids was shortest in the 7/04 trial under low PAR and temperature and longest in the 3/05 trial under high PAR and temperature (Table 7.1). Analyses of variation are to be found in following section 7.2.2. Low coefficients of variation were observed for days to mid-anthesis among months. Inbred Hi60, a temperate dent bred from Mo17 was earliest for days to mid-anthesis (55.5) across the four months. This inbred was originally selected for earliness to avoid frost damage in short temperate growing months. Mean days to mid-anthesis were earliest for Hybrids Hi53 x Hi60 and Hi60 x Hi67 (52.38 days), and latest for Hi65 x Hi26 (56.9 days) (Table 7.1).

Days to mid-silk was shortest in the 7/04 autumn trial and longest in the 3/05 summer trial among inbreds and hybrids (Table 7.2). Lower coefficients of variation were also observed for days to mid-silk among the four planting dates. Mean days to mid-silk across months was earliest for tropical flint inbred Hi67 (58.1 days) and latest for Hi26 (64.88 days). Silk emergence was earliest for hybrids Hi60 x Hi67 (53.3 days) and Hi53 x Hi60 (53.5) and latest for Hi65 x Hi26 (58.8 days) (Table 7.2).

Table 7.1. Mean days to mid-anthesis across planting dates.

Entry	Pedigree	7/04	8/04	3/05	5/05	Mean	Array
Inbreds	Inbreds						
Hi53	ICAL 210	52.5	56.5	67.0	56.5	58.13	54.09
Hi57	Ki9	53.0	58.0	67.0	57.0	58.75	54.57
Hi60	Mo17	50.5	53.0	64.5	54.0	55.50	53.48
Hi61	N3y	53.0	58.5	67.0	56.0	58.63	54.46
Hi62	Pi17	55.5	57.0	70.0	60.0	60.63	55.11
Hi65	Tx601	55.5	62.0	71.0	58.5	61.75	55.46
Hi67	Tzi18	52.5	53.5	66.0	55.5	56.88	53.93
Hi26	Hi26	56.5	60.5	70.5	61.0	62.13	55.57
Inbred mean	Means	53.6	57.4	67.9	57.3	59.05	
$LSD_{0.05}$ Inbreds		1.2	2.3	2.8	1.2	1.99	
Hybrids							
Hi53 x Hi57	ICAL 210 x Ki9	49.0	52.0	59.0	53.0	53.25	
Hi53 x Hi60	ICAL210 x Mo17	47.5	51.0	59.5	51.5	52.38	
Hi53 x Hi61	ICAL210 x N3y	52.0	53.5	64.0	54.0	55.88	
Hi53 x Hi62	ICAL210 x Pi17	49.5	52.0	62.0	53.5	54.25	
Hi53 x Hi65	ICAL210 x Tx601	50.5	53.0	61.0	54.0	54.63	
Hi53 x Hi67	ICAL210 x Tzi18	49.5	50.5	61.0	51.5	53.13	
Hi53 x Hi26	ICAL210 x Hi26	51.5	54.0	62.0	53.0	55.13	
Hi57 x Hi60	Ki9 x Mo17	49.0	51.0	62.0	52.5	53.63	
Hi57 x Hi61	Ki9 x N3y	50.0	52.5	60.5	53.5	54.13	
Hi57 x Hi62	Ki9 x Pi17	51.0	54.0	64.0	56.0	56.25	
Hi57 x Hi65	Ki9 x Tx601	52.0	53.5	63.0	54.0	55.63	
Hi57 x Hi67	Ki9 x Tzi18	49.5	51.5	63.0	54.0	54.50	
Hi57 x Hi26	Ki9 x Hi26	50.0	51.0	63.5	54.0	54.63	
Hi60 x Hi61	Mo17 x N3y	49.0	51.0	60.0	51.0	52.75	
Hi60 x Hi62	Mo17 x Pi17	49.5	52.0	61.5	51.5	53.63	
Hi60 x Hi65	Mo17 x Tx601	49.5	51.5	61.5	52.5	53.75	
Hi60 x Hi67	Mo17 x Tzi18	48.5	49.5	61.5	50.0	52.38	
Hi60 x Hi26	Mo17 x Hi26	52.0	54.0	62.5	55.0	55.88	
Hi61 x Hi62	N3y x Pi17	51.5	52.0	61.5	54.0	54.75	
Hi61 x Hi65	N3y x Tx601	51.5	54.5	63.0	54.5	55.88	
Hi61 x Hi67	N3y x Tzi18	50.0	50.5	60.5	51.5	53.13	
Hi61 x Hi26	N3y x Hi26	51.0	51.5	63.5	53.0	54.75	
Hi62 x Hi65	Pi17 x Tx601	52.0	53.5	64.5	55.0	56.25	
Hi62 x Hi67	Pi17 x Tzi18	50.5	52.5	59.5	53.5	54.00	
Hi62 x Hi26	Pi17 x Hi26	53.0	55.5	61.5	56.5	56.63	
Hi65 x Hi67	Tx601 x Tzi18	50.0	52.0	64.5	54.5	55.25	
Hi65 x Hi26	Tx601 x Hi26	52.5	56.0	62.5	56.5	56.88	
Hi67 x Hi26	Tzi18 x Hi26	51.0	50.5	64.0	55.0	55.13	
Hybrid mean		50.4	52.4	62.0	53.5	54.58	
$LSD_{0.05}$ Hybrids		1.7	2.2	3.4	2.0	2.40	
Grand Mean		51.2	53.5	63.3	54.4	55.58	
CV		1.4%	1.8%	2.4%	1.5%	1.88%	

Table 7.2. Mean days to mid-silk across planting dates.

Entry	Pedigree	7/04	8/04	3/05	5/05	Mean	Array
Inbreds							
Hi53	ICAL 210	52.5	56.0	67.0	57.5	58.25	55.50
Hi57	Ki9	52.5	56.5	70.0	56.0	58.75	55.57
Hi60	Mo17	53.0	56.0	67.0	57.5	58.38	54.66
Hi61	N3y	54.5	62.5	67.5	57.5	60.50	55.88
Hi62	Pi17	58.0	61.5	73.5	63.0	64.00	56.41
Hi65	Tx601	56.5	64.5	74.0	63.5	64.63	56.91
Hi67	Tzi18	52.0	56.5	68.5	55.5	58.13	55.20
Hi26	Hi26	58.5	63.5	73.0	64.5	64.88	57.23
Inbred mean	Means	54.7	59.6	70.1	59.4	60.94	
$LSD_{0.05}$ Inbreds		1.0	1.4	3.6	3.0	2.48	
Hybrids							
Hi53 x Hi57	ICAL 210 x Ki9	49.0	53.0	61.5	53.5	54.25	
Hi53 x Hi60	ICAL210 x Mo17	48.5	53.5	60.5	51.5	53.50	
Hi53 x Hi61	ICAL210 x N3y	53.0	57.0	66.5	57.0	58.38	
Hi53 x Hi62	ICAL210 x Pi17	49.0	53.5	64.0	54.5	55.25	
Hi53 x Hi65	ICAL210 x Tx601	51.5	55.5	61.0	54.0	55.50	
Hi53 x Hi67	ICAL210 x Tzi18	50.0	52.0	63.0	54.0	54.75	
Hi53 x Hi26	ICAL210 x Hi26	52.0	56.5	63.5	55.5	56.88	
Hi57 x Hi60	Ki9 x Mo17	49.0	53.5	63.0	53.0	54.63	
Hi57 x Hi61	Ki9 x N3y	49.5	53.5	61.0	53.0	54.25	
Hi57 x Hi62	Ki9 x Pi17	50.5	55.0	66.0	56.5	57.00	
Hi57 x Hi65	Ki9 x Tx601	52.5	56.0	65.0	55.5	57.25	
Hi57 x Hi67	Ki9 x Tzi18	49.5	54.0	63.0	55.5	55.50	
Hi57 x Hi26	Ki9 x Hi26	51.5	54.0	64.5	54.5	56.13	
Hi60 x Hi61	Mo17 x N3y	49.0	55.0	61.0	51.0	54.00	
Hi60 x Hi62	Mo17 x Pi17	49.5	54.5	63.0	53.5	55.13	
Hi60 x Hi65	Mo17 x Tx601	49.5	54.0	62.5	54.0	55.00	
Hi60 x Hi67	Mo17 x Tzi18	49.0	52.0	61.5	50.5	53.25	
Hi60 x Hi26	Mo17 x Hi26	52.0	56.5	64.0	56.0	57.13	
Hi61 x Hi62	N3y x Pi17	52.5	54.0	63.5	55.0	56.25	
Hi61 x Hi65	N3y x Tx601	52.0	56.5	63.5	56.0	57.00	
Hi61 x Hi67	N3y x Tzi18	50.0	54.0	61.5	52.0	54.38	
Hi61 x Hi26	N3y x Hi26	53.0	54.5	65.0	55.0	56.88	
Hi62 x Hi65	Pi17 x Tx601	53.5	56.0	66.5	57.0	58.25	
Hi62 x Hi67	Pi17 x Tzi18	51.0	55.0	60.0	54.0	55.00	
Hi62 x Hi26	Pi17 x Hi26	53.5	57.0	63.0	58.5	58.00	
Hi65 x Hi67	Tx601 x Tzi18	50.5	55.0	66.5	54.5	56.63	
Hi65 x Hi26	Tx601 x Hi26	53.0	58.5	64.5	59.0	58.75	
Hi67 x Hi26	Tzi18 x Hi26	52.0	54.5	66.0	55.0	56.88	
Hybrid mean		50.9	54.8	63.4	54.6	55.92	
$LSD_{0.05}$ Hybrids		1.5	2.1	3.9	2.4	2.63	
Grand Mean		51.8	55.9	64.9	55.7	57.03	
CV		1.2%	1.6%	2.8%	2.1%	2.10%	

7.2.1.2 Ear height and plant height

Ear heights varied among the four planting dates for inbreds and hybrids with low coefficients of variation (Table 7.3). Among inbreds mean ear heights were shorter in 8/04 (70 cm) under low PAR and temperature and taller (103.9 cm) in the 7/04 summer planting. Mean ear heights for hybrids were also highest in 7/04 (139.6 cm) and lowest in 3/05 (111.2 cm). Across months, ear heights of inbreds ranged from 72.6 cm (Hi60) to 91.8 (Hi57). Inbred Hi57 was bred from a tropical flint Ku1409 originating from the Suwan population. Hybrids characterized by low ear heights had Hi60 as one of the parents (Table 7.3).

Plant heights varied also among the four Waimanalo months for both inbreds and hybrids with low coefficients of variation (Table 7.4). Inbreds were tallest in the 7/04 trial and shortest in the 8/04 trial. Inbred Hi61 a highland tropical dent was tallest across months (186.6 cm), while inbred Hi67 a tropical flint, was the shortest (149.1 cm). Mean plant heights of hybrids were also taller in 7/04 and shorter in the autumn trial (8/04), under low PAR and temperature. Tallest stature hybrid was Hi61 x Hi65 (253.5 cm) and shortest was Hi60 x Hi62 (210.6 cm) (Table 7.4). Most hybrids having Hi61 as parent were taller than the average (> 229.5 cm).

Table 7.3. Mean ear height (cm) across planting dates.

Entry	Pedigree	7/04	8/04	3/05	5/05	Mean	Array
Inbreds							
Hi53	ICAL 210	97.5	85.5	60.0	76.5	79.88	125.99
Hi57	Ki9	114.0	76.5	78.5	98.0	91.75	125.82
Hi60	Mo17	89.5	60.0	67.0	73.8	72.56	110.48
Hi61	N3y	101.0	52.8	77.8	83.0	78.63	122.98
Hi62	Pi17	109.0	75.3	75.5	91.3	87.75	125.68
Hi65	Tx601	126.0	61.8	85.5	89.0	90.55	130.59
Hi67	Tzi18	84.0	78.5	63.3	71.3	74.25	117.83
Hi26	Hi26	110.5	69.5	88.5	88.0	89.13	125.57
Inbred mean		103.9	70.0	74.5	83.8	83.06	
$LSD_{0.05}$ Inbreds		10.0	15.5	14.2	17.6	14.57	
Hybrids							
Hi53 x Hi57	ICAL 210 x Ki9	145.5	120.5	109.3	138.5	128.44	
Hi53 x Hi60	ICAL210 x Mo17	122.0	99.5	88.5	106.3	104.06	
Hi53 x Hi61	ICAL210 x N3y	176.0	134.5	134.3	139.8	146.13	
Hi53 x Hi62	ICAL210 x Pi17	139.5	128.8	108.8	122.3	124.81	
Hi53 x Hi65	ICAL210 x Tx601	148.0	128.0	124.8	133.0	133.44	
Hi53 x Hi67	ICAL210 x Tzi18	133.0	121.0	100.3	123.8	119.50	
Hi53 x Hi26	ICAL210 x Hi26	148.0	117.5	111.3	125.5	125.56	
Hi57 x Hi60	Ki9 x Mo17	128.0	105.5	83.5	113.3	107.56	
Hi57 x Hi61	Ki9 x N3y	148.5	117.8	113.0	123.3	125.63	
Hi57 x Hi62	Ki9 x Pi17	151.5	125.5	113.3	133.5	130.94	
Hi57 x Hi65	Ki9 x Tx601	149.0	131.5	139.8	137.8	139.50	
Hi57 x Hi67	Ki9 x Tzi18	135.0	116.8	115.5	123.5	122.69	
Hi57 x Hi26	Ki9 x Hi26	144.0	117.3	116.8	126.0	126.00	
Hi60 x Hi61	Mo17 x N3y	126.0	97.5	105.8	109.5	109.69	
Hi60 x Hi62	Mo17 x Pi17	123.5	104.5	97.3	109.0	108.56	
Hi60 x Hi65	Mo17 x Tx601	125.5	106.3	104.3	126.0	115.50	
Hi60 x Hi67	Mo17 x Tzi18	118.5	101.0	108.5	112.0	110.00	
Hi60 x Hi26	Mo17 x Hi26	132.0	110.8	114.3	115.0	118.00	
Hi61 x Hi62	N3y x Pi17	149.0	115.0	111.5	123.0	124.63	
Hi61 x Hi65	N3y x Tx601	150.0	115.5	114.5	132.5	128.13	
Hi61 x Hi67	N3y x Tzi18	127.5	103.8	89.0	104.5	106.19	
Hi61 x Hi26	N3y x Hi26	148.0	110.3	104.5	119.3	120.50	
Hi62 x Hi65	Pi17 x Tx601	145.0	133.3	116.8	144.3	134.81	
Hi62 x Hi67	Pi17 x Tzi18	130.5	113.5	118.0	125.8	121.94	
Hi62 x Hi26	Pi17 x Hi26	146.5	121.0	129.8	139.0	134.06	
Hi65 x Hi67	Tx601 x Tzi18	137.5	122.5	107.0	137.8	126.19	
Hi65 x Hi26	Tx601 x Hi26	154.5	124.8	129.0	138.0	136.56	
Hi67 x Hi26	Tzi18 x Hi26	127.5	112.0	104.0	129.8	118.31	
Hybrid mean		139.6	116.3	111.2	125.4	123.12	
$LSD_{0.05}$ Hybrids		13.5	17.0	17.8	12.5	15.35	
Grand mean		131.7	106.0	103.0	116.2	114.22	
CV		4.4%	6.9%	7.3%	5.2%	5.85%	

Table 7.4. Mean plant height (cm) across planting dates.

Entry	Pedigree	7/04	8/04	3/05	5/05	Mean	Array
Inbreds							
Hi53	ICAL 210	173.3	160.8	141.8	162.3	159.50	228.70
Hi57	Ki9	176.0	138.5	146.5	169.5	157.63	225.04
Hi60	Mo17	171.8	151.5	154.3	168.3	161.44	220.42
Hi61	N3y	210.5	144.5	189.5	202.0	186.63	238.43
Hi62	Pi17	183.8	151.5	164.8	176.5	169.13	227.53
Hi65	Tx601	209.8	142.0	184.1	183.8	179.90	242.19
Hi67	Tzi18	162.8	151.3	137.5	145.0	149.13	220.00
Hi26	Hi26	197.0	142.3	169.3	173.5	170.50	233.49
Inbred mean		185.6	147.8	161.0	172.6	166.73	
$LSD_{0.05}$ Inbreds		11.8	18.5	21.4	24.9	19.72	
Hybrids							
Hi53 x Hi57	ICAL 210 x Ki9	233.5	206.0	203.5	235.0	219.50	
Hi53 x Hi60	ICAL210 x Mo17	226.5	199.3	200.8	223.5	212.50	
Hi53 x Hi61	ICAL210 x N3y	274.8	231.0	242.3	249.0	249.25	
Hi53 x Hi62	ICAL210 x Pi17	243.8	218.3	201.3	226.8	222.50	
Hi53 x Hi65	ICAL210 x Tx601	260.3	227.0	238.3	243.3	242.19	
Hi53 x Hi67	ICAL210 x Tzi18	233.0	220.3	201.5	230.5	221.31	
Hi53 x Hi26	ICAL210 x Hi26	251.0	213.3	227.5	242.8	233.63	
Hi57 x Hi60	Ki9 x Mo17	232.8	206.3	186.5	224.5	212.50	
Hi57 x Hi61	Ki9 x N3y	247.8	223.0	223.0	238.3	233.00	
Hi57 x Hi62	Ki9 x Pi17	242.0	213.0	208.5	233.0	224.13	
Hi57 x Hi65	Ki9 x Tx601	266.0	224.8	236.3	249.5	244.13	
Hi57 x Hi67	Ki9 x Tzi18	231.0	200.8	212.0	224.0	216.94	
Hi57 x Hi26	Ki9 x Hi26	241.5	209.0	222.0	228.0	225.13	
Hi60 x Hi61	Mo17 x N3y	243.8	214.0	235.5	228.3	230.38	
Hi60 x Hi62	Mo17 x Pi17	217.3	197.0	203.3	224.8	210.56	
Hi60 x Hi65	Mo17 x Tx601	233.3	231.8	224.8	245.0	233.69	
Hi60 x Hi67	Mo17 x Tzi18	227.8	199.3	206.8	217.0	212.69	
Hi60 x Hi26	Mo17 x Hi26	242.0	209.5	236.5	234.5	230.63	
Hi61 x Hi62	N3y x Pi17	267.8	220.0	226.5	251.0	241.31	
Hi61 x Hi65	N3y x Tx601	269.0	224.3	247.8	272.3	253.31	
Hi61 x Hi67	N3y x Tzi18	252.3	216.8	204.8	222.3	224.00	
Hi61 x Hi26	N3y x Hi26	269.8	214.3	224.3	242.8	237.75	
Hi62 x Hi65	Pi17 x Tx601	254.8	225.8	225.0	257.0	240.63	
Hi62 x Hi67	Pi17 x Tzi18	219.8	200.3	215.7	223.3	214.73	
Hi62 x Hi26	Pi17 x Hi26	254.8	212.8	240.3	247.8	238.88	
Hi65 x Hi67	Tx601 x Tzi18	245.3	216.3	220.3	244.8	231.63	
Hi65 x Hi26	Tx601 x Hi26	262.8	221.5	259.8	255.0	249.75	
Hi67 x Hi26	Tzi18 x Hi26	238.5	203.3	203.8	229.3	218.69	
Hybrid mean		245.8	214.2	220.6	237.2	229.47	
$LSD_{0.05}$ Hybrids		13.2	21.1	25.7	17.5	19.89	
Grand mean		232.4	199.5	207.4	222.9	215.53	
CV		2.4%	4.5%	5.3%	3.8%	4.05%	

7.2.1.3 Ear diameter and ear length

Ear diameters among inbreds and hybrids were characterized by low coefficients of variation among the four months and the combined analysis (Table 7.5). Mean ear diameters were least in the autumn trial (8/4) for both inbreds and hybrids. Ear diameters were similar for the trials in 7/04 and the two summer trials in 2005. Across months mean ear diameter was least for inbred Hi61 (3.4 cm) and highest for Hi57 (4.4 cm). Hybrids Hi57 x Hi65 (5.2 cm) and Hi62 x Hi65 (5.1 cm) were characterized by larger ear diameters (Table 7.5).

Ear lengths varied among the four months for both inbreds and hybrids with low coefficients of variation (Table 7.6). Ear lengths were shorter in the autumn month in 8/04 under low PAR and temperature among inbreds and hybrids. In 8/04, mean ear length was 11.4 cm among inbreds and 15.2 cm among hybrids (Table 7.6). Mean ear lengths were similar in 7/04 and the 2005 summer trials. Inbred Hi60 had the mean longest ears (16.9 cm) across months. Inbred Hi26 was characterized with shorter ears. Hybrids with exceptionally long ears had occasionally Hi53, Hi60 and Hi61 as either parent. Hybrid with the longest mean ear length was Hi60 x Hi67 (Table 7.6).

Table 7.5. Mean ear diameter (cm) across planting dates.

Entry	Pedigree	7/04	8/04	3/05	5/05	Mean	Array
Inbreds							
Hi53	ICAL 210	4.4	4.0	4.1	4.2	4.15	4.74
Hi57	Ki9	4.4	4.3	4.5	4.5	4.42	4.82
Hi60	Mo17	3.9	3.0	3.5	4.0	3.57	4.27
Hi61	N3y	3.7	2.7	3.6	3.7	3.39	4.47
Hi62	Pi17	4.2	3.8	4.3	4.6	4.20	4.75
Hi65	Tx601	4.8	3.0	4.6	4.3	4.15	4.82
Hi67	Tzi18	4.1	3.8	4.0	4.0	3.97	4.65
Hi26	Hi26	3.9	3.1	3.9	3.7	3.64	4.58
Inbred mean		4.2	3.4	4.1	4.1	3.94	
$LSD_{0.05}$ Inbreds		0.4	0.3	0.3	0.6	0.42	
Hybrids							
Hi53 x Hi57	ICAL 210 x Ki9	5.1	4.8	5.0	5.0	4.95	
Hi53 x Hi60	ICAL210 x Mo17	4.6	3.9	4.5	4.5	4.35	
Hi53 x Hi61	ICAL210 x N3y	4.8	4.3	5.1	4.9	4.76	
Hi53 x Hi62	ICAL210 x Pi17	5.0	4.7	5.0	5.1	4.93	
Hi53 x Hi65	ICAL210 x Tx601	5.1	4.7	5.1	4.9	4.93	
Hi53 x Hi67	ICAL210 x Tzi18	4.6	4.4	4.7	4.9	4.63	
Hi53 x Hi26	ICAL210 x Hi26	4.7	4.2	4.9	4.9	4.67	
Hi57 x Hi60	Ki9 x Mo17	4.3	4.3	4.3	4.5	4.31	
Hi57 x Hi61	Ki9 x N3y	4.7	4.4	4.7	4.9	4.68	
Hi57 x Hi62	Ki9 x Pi17	4.9	4.7	5.0	5.1	4.90	
Hi57 x Hi65	Ki9 x Tx601	5.4	4.9	5.3	5.2	5.19	
Hi57 x Hi67	Ki9 x Tzi18	5.1	4.8	5.0	5.1	4.98	
Hi57 x Hi26	Ki9 x Hi26	4.7	4.6	4.9	5.0	4.76	
Hi60 x Hi61	Mo17 x N3y	4.2	3.3	4.3	4.5	4.05	
Hi60 x Hi62	Mo17 x Pi17	4.6	4.1	4.5	4.6	4.43	
Hi60 x Hi65	Mo17 x Tx601	4.4	3.7	4.3	4.5	4.21	
Hi60 x Hi67	Mo17 x Tzi18	4.7	3.6	4.3	4.5	4.25	
Hi60 x Hi26	Mo17 x Hi26	4.4	3.8	4.7	4.4	4.33	
Hi61 x Hi62	N3y x Pi17	4.7	4.1	4.7	4.6	4.51	
Hi61 x Hi65	N3y x Tx601	4.8	3.9	4.9	4.9	4.62	
Hi61 x Hi67	N3y x Tzi18	4.4	4.0	4.5	4.7	4.38	
Hi61 x Hi26	N3y x Hi26	4.5	3.8	4.5	4.5	4.29	
Hi62 x Hi65	Pi17 x Tx601	5.2	4.7	5.2	5.2	5.08	
Hi62 x Hi67	Pi17 x Tzi18	4.8	4.8	4.8	4.7	4.78	
Hi62 x Hi26	Pi17 x Hi26	4.7	4.2	4.7	5.0	4.63	
Hi65 x Hi67	Tx601 x Tzi18	5.3	4.4	5.0	5.1	4.96	
Hi65 x Hi26	Tx601 x Hi26	4.9	4.3	5.1	5.1	4.80	
Hi67 x Hi26	Tzi18 x Hi26	4.8	4.2	4.7	4.8	4.60	
Hybrid mean		4.7	4.3	4.8	4.8	4.64	
$LSD_{0.05}$ Hybrids		0.4	0.4	0.3	0.3	0.35	
Grand Mean		4.6	4.1	4.6	4.7	4.48	
CV		3.6%	3.9%	2.9%	4.1%	3.66%	

Table 7.6. Mean ear length (cm) across planting dates.

Entry	Pedigree	7/04	8/04	3/05	5/05	EL	Array
Inbreds							
Hi53	ICAL 210	16.9	12.0	16.8	14.3	14.97	18.97
Hi57	Ki9	16.5	11.5	16.6	16.5	15.28	18.21
Hi60	Mo17	17.9	13.3	18.1	18.2	16.86	19.63
Hi61	N3y	16.7	11.2	18.0	17.5	15.84	18.82
Hi62	Pi17	14.0	11.4	12.9	13.1	12.84	17.37
Hi65	Tx601	16.1	9.4	14.0	11.7	12.78	17.66
Hi67	Tzi18	17.6	12.3	16.5	16.6	15.74	18.51
Hi26	Hi26	17.2	10.3	13.5	15.7	14.19	18.98
Inbred mean		16.6	11.4	15.8	15.5	14.81	
$LSD_{0.05}$ Inbreds		2.0	2.0	2.7	3.2	2.52	
Hybrids							
Hi53 x Hi57	ICAL 210 x Ki9	19.3	14.7	19.1	18.5	17.88	
Hi53 x Hi60	ICAL210 x Mo17	21.7	17.5	21.7	20.9	20.45	
Hi53 x Hi61	ICAL210 x N3y	21.5	14.3	21.6	21.6	19.73	
Hi53 x Hi62	ICAL210 x Pi17	17.6	14.4	18.4	18.5	17.20	
Hi53 x Hi65	ICAL210 x Tx601	19.9	14.9	20.2	18.7	18.38	
Hi53 x Hi67	ICAL210 x Tzi18	19.6	15.9	20.1	21.0	19.13	
Hi53 x Hi26	ICAL210 x Hi26	22.6	16.3	20.8	20.5	20.03	
Hi57 x Hi60	Ki9 x Mo17	21.2	17.8	19.5	21.1	19.86	
Hi57 x Hi61	Ki9 x N3y	20.0	14.4	19.4	19.6	18.32	
Hi57 x Hi62	Ki9 x Pi17	17.7	13.8	17.3	17.4	16.53	
Hi57 x Hi65	Ki9 x Tx601	20.8	15.6	18.5	17.3	18.03	
Hi57 x Hi67	Ki9 x Tzi18	19.0	14.9	18.6	18.6	17.78	
Hi57 x Hi26	Ki9 x Hi26	21.3	15.9	20.0	19.1	19.06	
Hi60 x Hi61	Mo17 x N3y	21.6	14.8	21.6	21.6	19.88	
Hi60 x Hi62	Mo17 x Pi17	19.9	15.6	19.2	19.8	18.60	
Hi60 x Hi65	Mo17 x Tx601	19.8	13.5	19.1	20.1	18.11	
Hi60 x Hi67	Mo17 x Tzi18	22.1	19.4	20.0	22.7	21.03	
Hi60 x Hi26	Mo17 x Hi26	20.6	16.1	21.5	19.9	19.51	
Hi61 x Hi62	N3y x Pi17	20.1	15.2	18.9	18.8	18.23	
Hi61 x Hi65	N3y x Tx601	19.5	11.3	18.5	20.0	17.30	
Hi61 x Hi67	N3y x Tzi18	20.5	16.7	19.5	21.1	19.43	
Hi61 x Hi26	N3y x Hi26	21.1	14.4	20.0	20.0	18.86	
Hi62 x Hi65	Pi17 x Tx601	19.4	13.0	18.1	17.1	16.87	
Hi62 x Hi67	Pi17 x Tzi18	17.5	13.5	17.0	16.9	16.19	
Hi62 x Hi26	Pi17 x Hi26	19.9	15.3	18.6	18.2	17.98	
Hi65 x Hi67	Tx601 x Tzi18	18.8	13.9	16.6	17.7	16.73	
Hi65 x Hi26	Tx601 x Hi26	19.9	14.4	18.9	19.6	18.18	
Hi67 x Hi26	Tzi18 x Hi26	20.7	17.1	19.1	20.2	19.26	
Hybrid mean		20.1	15.2	19.3	19.5	18.52	
$LSD_{0.05}$ Hybrids		2.2	2.9	1.8	2.3	2.33	
Grand Mean		19.3	14.3	18.5	18.6	17.69	
CV		5.0%	8.3%	4.6%	6.2%	5.91%	

7.2.1.4 Kernel number and kernel row number

Kernel numbers were characterized by low coefficients of variation among the summer trials except for the autumn trial in 8/04 (CV = 9.9%) (Table 7.7). Mean kernel numbers were lower in the autumn trial in 8/04 characterized by low PAR and temperature and were higher in the 7/04 and 2005 summer trials under high PAR and temperature among inbreds and hybrids. In 8/04 mean kernel number among inbreds was 19.9, while mean kernel number among hybrids was 30.4. Inbreds Hi57, Hi60 and Hi67 were characterized by high kernel numbers (Table 7.4). Among hybrids, mean kernel numbers ranged from 31.93 (Hi53 x Hi57) to 41.8 (Hi60 x Hi65). Hybrid Hi53 x Hi57 is a tropical flint x tropical flint cross, while Hi60 x Hi65 is a temperate dent x tropical flint.

Kernel row numbers varied among inbreds and hybrids among the four Waimanalo months with low coefficients of variation (Table 7.8). Mean kernel row numbers were lowest in the autumn planting in 8/04 among inbreds and hybrids. Inbred Hi61 a tropical highland dent had the lowest kernel row number, while Hi57, Hi65 and Hi67 had high kernel row numbers (Table 7.8). Higher kernel row numbers were observed in some hybrids with Hi53, Hi57, Hi65 and Hi67. Hybrids Hi57 x Hi65 and Hi57 x Hi67 had the most kernel row numbers (16.1).

Table 7.7. Mean kernel number across planting dates.

Entry	Pedigree	7/04	8/04	3/05	5/05	Mean	Array
Inbreds							
Hi53	ICAL 210	28.3	19.4	25.1	25.1	24.48	35.36
Hi57	Ki9	29.1	20.7	28.6	29.3	26.93	35.68
Hi60	Mo17	30.9	24.3	28.4	27.5	27.76	39.77
Hi61	N3y	26.7	17.2	28.8	30.2	25.73	36.25
Hi62	Pi17	29.4	22.2	26.9	28.5	26.75	36.35
Hi65	Tx601	31.3	16.2	31.9	26.8	26.55	38.28
Hi67	Tzi18	30.7	24.7	30.2	31.7	29.33	36.23
Hi26	Hi26	20.7	14.4	18.6	21.5	18.80	38.34
Inbred mean		28.4	19.9	27.3	27.6	25.79	
$LSD_{0.05}$ Inbreds		6.8	4.2	3.3	5.3	5.07	
Hi53 x Hi57	ICAL 210 x Ki9	36.7	24.4	34.0	32.6	31.93	
Hi53 x Hi60	ICAL210 x Mo17	39.1	34.1	44.1	39.9	39.30	
Hi53 x Hi61	ICAL210 x N3y	39.6	30.6	40.9	39.1	37.55	
Hi53 x Hi62	ICAL210 x Pi17	36.3	26.9	34.9	34.4	33.13	
Hi53 x Hi65	ICAL210 x Tx601	41.0	29.6	40.4	34.8	36.45	
Hi53 x Hi67	ICAL210 x Tzi18	35.9	25.0	35.9	38.9	33.93	
Hi53 x Hi26	ICAL210 x Hi26	39.1	28.1	37.1	36.8	35.27	
Hi57 x Hi60	Ki9 x Mo17	39.6	32.5	39.6	42.5	38.55	
Hi57 x Hi61	Ki9 x N3y	38.1	25.9	36.2	36.0	34.06	
Hi57 x Hi62	Ki9 x Pi17	36.7	28.9	36.5	36.3	34.60	
Hi57 x Hi65	Ki9 x Tx601	44.3	34.6	40.3	37.2	39.10	
Hi57 x Hi67	Ki9 x Tzi18	36.3	29.7	35.3	35.8	34.28	
Hi57 x Hi26	Ki9 x Hi26	42.3	30.4	39.2	37.1	37.25	
Hi60 x Hi61	Mo17 x N3y	42.5	27.4	43.7	43.6	39.29	
Hi60 x Hi62	Mo17 x Pi17	40.7	32.0	41.2	41.3	38.80	
Hi60 x Hi65	Mo17 x Tx601	44.7	31.9	43.9	46.8	41.81	
Hi60 x Hi67	Mo17 x Tzi18	42.0	36.5	39.5	42.2	40.06	
Hi60 x Hi26	Mo17 x Hi26	41.2	32.3	45.7	43.2	40.59	
Hi61 x Hi62	N3y x Pi17	39.0	32.3	38.4	37.1	36.70	
Hi61 x Hi65	N3y x Tx601	38.7	24.1	36.8	39.2	34.70	
Hi61 x Hi67	N3y x Tzi18	38.7	29.4	37.3	37.4	35.69	
Hi61 x Hi26	N3y x Hi26	37.9	28.8	38.9	37.5	35.78	
Hi62 x Hi65	Pi17 x Tx601	43.3	30.2	40.2	36.0	37.43	
Hi62 x Hi67	Pi17 x Tzi18	33.8	29.1	36.0	36.3	33.80	
Hi62 x Hi26	Pi17 x Hi26	41.1	35.7	41.5	41.6	39.98	
Hi65 x Hi67	Tx601 x Tzi18	40.6	33.1	35.4	40.6	37.43	
Hi65 x Hi26	Tx601 x Hi26	44.1	33.8	42.0	44.4	41.08	
Hi67 x Hi26	Tzi18 x Hi26	41.2	34.1	37.4	41.0	38.43	
Hybrid mean		39.8	30.4	39.0	38.9	37.03	
$LSD_{0.05}$ Hybrids		4.4	6.8	4.9	4.8	5.32	
Grand mean		37.3	28.1	36.4	36.4	34.53	
CV		6.1%	9.9%	5.7%	6.2%	6.84%	

Table 7.8. Mean kernel row number across planting dates.

Entry	Pedigree	7/04	8/04	3/05	5/05	KRN	Array
Inbreds							
Hi53	ICAL 210	14.0	12.5	11.9	13.2	12.9	13.90
Hi57	Ki9	15.0	13.8	14.4	15.4	14.7	14.52
Hi60	Mo17	11.4	9.8	10.0	10.5	10.4	12.41
Hi61	N3y	10.4	8.8	10.0	9.8	9.8	12.35
Hi62	Pi17	12.6	12.4	13.0	13.2	12.8	13.38
Hi65	Tx601	15.6	10.8	15.4	16.0	14.4	14.40
Hi67	Tzi18	13.8	15.0	15.7	14.2	14.7	14.52
Hi26	Hi26	12.4	11.4	12.7	12.8	12.3	13.37
Inbred mean		13.2	11.8	12.9	13.1	12.7	
$LSD_{0.05}$ Inbreds		1.5	2.1	1.1	1.1	1.5	
Hi53 x Hi57	ICAL 210 x Ki9	14.6	14.2	14.6	15.0	14.6	
Hi53 x Hi60	ICAL210 x Mo17	13.2	12.4	12.2	13.2	12.8	
Hi53 x Hi61	ICAL210 x N3y	13.2	12.6	12.8	13.6	13.1	
Hi53 x Hi62	ICAL210 x Pi17	14.4	13.8	13.2	13.8	13.8	
Hi53 x Hi65	ICAL210 x Tx601	14.8	14.6	14.6	14.2	14.6	
Hi53 x Hi67	ICAL210 x Tzi18	14.6	14.6	14.2	14.8	14.6	
Hi53 x Hi26	ICAL210 x Hi26	14.0	13.0	14.0	14.9	14.0	
Hi57 x Hi60	Ki9 x Mo17	13.0	13.6	12.8	13.6	13.3	
Hi57 x Hi61	Ki9 x N3y	12.9	12.8	13.2	13.8	13.2	
Hi57 x Hi62	Ki9 x Pi17	14.4	15.0	14.4	14.8	14.7	
Hi57 x Hi65	Ki9 x Tx601	16.2	15.4	16.2	16.4	16.1	
Hi57 x Hi67	Ki9 x Tzi18	16.4	15.6	15.6	16.8	16.1	
Hi57 x Hi26	Ki9 x Hi26	14.0	14.0	13.4	13.8	13.8	
Hi60 x Hi61	Mo17 x N3y	10.0	9.8	10.6	11.1	10.4	
Hi60 x Hi62	Mo17 x Pi17	12.0	12.4	11.6	12.4	12.1	
Hi60 x Hi65	Mo17 x Tx601	12.6	12.8	12.3	13.0	12.7	
Hi60 x Hi67	Mo17 x Tzi18	14.4	12.8	13.2	13.6	13.5	
Hi60 x Hi26	Mo17 x Hi26	11.4	12.5	12.8	12.4	12.3	
Hi61 x Hi62	N3y x Pi17	12.0	12.0	11.8	12.0	12.0	
Hi61 x Hi65	N3y x Tx601	13.2	12.3	13.4	13.6	13.1	
Hi61 x Hi67	N3y x Tzi18	12.6	13.2	12.6	13.6	13.0	
Hi61 x Hi26	N3y x Hi26	11.6	11.8	11.4	12.4	11.8	
Hi62 x Hi65	Pi17 x Tx601	14.7	13.6	14.4	14.4	14.3	
Hi62 x Hi67	Pi17 x Tzi18	14.4	14.6	14.6	14.0	14.4	
Hi62 x Hi26	Pi17 x Hi26	12.6	12.2	12.0	13.2	12.5	
Hi65 x Hi67	Tx601 x Tzi18	15.4	15.6	15.2	15.8	15.5	
Hi65 x Hi26	Tx601 x Hi26	15.0	13.8	14.8	15.0	14.7	
Hi67 x Hi26	Tzi18 x Hi26	14.4	14.2	14.8	15.0	14.6	
Hybrid mean		13.6	13.4	13.5	13.9	13.6	
$LSD_{0.05}$ Hybrids		1.3	1.3	1.7	1.7	1.5	
Grand mean		13.5	13.0	13.3	13.8	13.4	
CV		4.9%	5.0%	5.3%	5.1%	5.08%	

7.2.1.5 Kernel weight and plant yield

Mean kernel weights varied among the four months among inbreds and hybrids. Kernel weights were highest in the 5/05 trial and lowest in the 8/04 trial for both inbreds and hybrids (Table 7.9). Coefficients of variation was high in 8/04 (CV = 10.3%) under inadequate PAR and low temperature month which was greatly improved in the summer trials in 7/04 and in 2005. Mean kernel weights among inbreds ranged from 105.2 g (Hi67) to 152.2 g (Hi61) across months. Higher kernel weights were observed in crosses with tropical dent Hi61 in combination with some tropical flint inbreds. For example kernel weight was highest in Hi61 x Hi62 (197.7 g), dent x flint cross (Table 7.9).

Plant yields among inbreds and hybrids varied with moderately high coefficients of variation among the four months (Table 7.10). As it was for most traits, mean ear weights were lowest in the autumn trial in 8/04 and highest in the summer trial in 7/04 and in 2005. Relative to the autumn trial in 8.04, mean plant yields were two times higher in the summer trials. Among inbreds, mean ear weights across months ranged from 11.8 g (Hi26) to 25.4 g (Hi57). Mean ear weights among hybrids were similar for the summer trials in 7/04, 3/05 and 5/05. Hybrid Hi57 x Hi65 had the highest mean ear weight (49.8 g) followed by Hi57 x Hi26 (45.5 g) across the four months (Table 7.10). Hybrids characterized by tropical flint x tropical dent parents had generally heavier ear weights.

Table 7.9. Mean kernel weight (g) across planting dates.

Cross	Pedigree	7/04	8/04	3/05	5/05	KW	Array
Inbreds							
Hi53	ICAL 210	146.3	139.1	155.4	151.9	148.14	175.65
Hi57	Ki9	144.2	136.7	141.6	156.3	144.70	168.14
Hi60	Mo17	146.7	74.0	125.7	142.5	122.19	158.50
Hi61	N3y	181.2	65.1	173.0	189.6	152.20	183.97
Hi62	Pi17	143.8	98.9	124.8	129.7	124.27	171.38
Hi65	Tx601	133.3	83.1	112.9	116.1	111.34	154.29
Hi67	Tzi18	119.5	86.0	99.8	115.4	105.15	155.58
Hi26	Hi26	147.1	71.6	141.9	141.4	125.48	164.75
Inbred mean		145.3	94.3	134.3	142.8	129.18	
$LSD_{0.05}$ Inbreds		8.8	36.1	14.0	6.1	20.09	
Hybrids							
Hi53 x Hi57	ICAL 210 x Ki9	178.1	168.1	173.6	185.7	176.37	
Hi53 x Hi60	ICAL210 x Mo17	180.5	112.7	174.0	183.5	162.68	
Hi53 x Hi61	ICAL210 x N3y	199.3	136.9	211.1	226.9	193.50	
Hi53 x Hi62	ICAL210 x Pi17	177.4	159.6	192.7	201.4	182.76	
Hi53 x Hi65	ICAL210 x Tx601	176.4	146.8	177.4	187.1	171.90	
Hi53 x Hi67	ICAL210 x Tzi18	172.1	142.3	164.6	186.7	166.39	
Hi53 x Hi26	ICAL210 x Hi26	190.8	133.8	184.9	194.3	175.94	
Hi57 x Hi60	Ki9 x Mo17	167.9	139.9	149.2	171.0	156.98	
Hi57 x Hi61	Ki9 x N3y	194.3	176.9	190.7	212.4	193.54	
Hi57 x Hi62	Ki9 x Pi17	164.0	141.1	167.8	181.0	163.45	
Hi57 x Hi65	Ki9 x Tx601	156.8	135.6	156.5	171.9	155.17	
Hi57 x Hi67	Ki9 x Tzi18	161.2	134.0	150.4	170.2	153.94	
Hi57 x Hi26	Ki9 x Hi26	174.1	150.6	182.1	203.3	177.51	
Hi60 x Hi61	Mo17 x N3y	204.6	106.9	206.2	230.3	187.00	
Hi60 x Hi62	Mo17 x Pi17	195.1	119.8	176.8	201.3	173.24	
Hi60 x Hi65	Mo17 x Tx601	151.2	66.7	134.7	159.9	128.10	
Hi60 x Hi67	Mo17 x Tzi18	175.8	92.1	146.1	183.7	149.41	
Hi60 x Hi26	Mo17 x Hi26	169.7	68.9	175.2	194.5	152.07	
Hi61 x Hi62	N3y x Pi17	207.5	137.1	216.6	229.6	197.70	
Hi61 x Hi65	N3y x Tx601	182.2	99.5	192.5	209.9	171.01	
Hi61 x Hi67	N3y x Tzi18	180.3	115.4	177.8	200.0	168.37	
Hi61 x Hi26	N3y x Hi26	196.6	97.7	199.1	213.5	176.69	
Hi62 x Hi65	Pi17 x Tx601	172.9	136.9	174.0	185.9	167.39	
Hi62 x Hi67	Pi17 x Tzi18	158.7	119.6	154.5	162.7	148.86	
Hi62 x Hi26	Pi17 x Hi26	188.4	114.7	175.6	186.3	166.24	
Hi65 x Hi67	Tx601 x Tzi18	164.2	103.5	142.1	157.9	141.89	
Hi65 x Hi26	Tx601 x Hi26	148.7	88.9	162.6	178.3	144.59	
Hi67 x Hi26	Tzi18 x Hi26	178.7	119.3	160.3	182.7	160.24	
Hybrid mean		177.4	123.7	173.9	191.1	166.53	
$LSD_{0.05}$ Hybrids		25.6	24.3	18.6	14.4	21.21	
Grand Mean		170.3	117.2	165.1	180.4	158.23	
CV		6.0%	10.4%	4.7%	3.4%	5.97%	

Table 7.10. Mean plant yield (g) across planting dates.

Entry	Pedigree	7/04	8/04	3/05	5/05	Yield	Array
Inbreds							
Hi53	ICAL 210	26.1	14.1	24.0	20.4	21.15	41.09
Hi57	Ki9	25.5	17.8	28.0	30.2	25.36	42.73
Hi60	Mo17	33.3	7.3	17.4	17.3	18.82	35.50
Hi61	N3y	21.1	5.2	23.3	22.3	17.98	38.82
Hi62	Pi17	22.7	11.5	22.1	20.0	19.05	38.63
Hi65	Tx601	31.3	4.5	25.7	21.5	20.75	41.43
Hi67	Tzi18	23.8	13.7	22.2	24.1	20.96	39.21
Hi26	Hi26	15.6	4.8	14.0	12.8	11.77	40.19
Inbred mean		24.92	9.85	22.08	21.06	19.48	
$LSD_{0.05}$ Inbreds		10.75	2.41	4.68	4.83	6.45	
Hybrids							
Hi53 x Hi57	ICAL 210 x Ki9	45.6	30.4	44.7	43.8	41.11	
Hi53 x Hi60	ICAL210 x Mo17	42.1	20.6	44.0	43.2	37.46	
Hi53 x Hi61	ICAL210 x N3y	47.1	21.6	53.1	52.2	43.49	
Hi53 x Hi62	ICAL210 x Pi17	43.0	29.7	46.5	45.1	41.06	
Hi53 x Hi65	ICAL210 x Tx601	49.6	28.9	51.5	42.2	43.03	
Hi53 x Hi67	ICAL210 x Tzi18	39.5	25.6	42.0	50.7	39.48	
Hi53 x Hi26	ICAL210 x Hi26	49.0	24.1	48.9	45.9	41.97	
Hi57 x Hi60	Ki9 x Mo17	39.3	30.4	36.2	44.1	37.51	
Hi57 x Hi61	Ki9 x N3y	52.6	27.6	46.5	47.6	43.59	
Hi57 x Hi62	Ki9 x Pi17	41.1	29.7	43.8	43.7	39.55	
Hi57 x Hi65	Ki9 x Tx601	58.5	36.1	54.3	50.3	49.79	
Hi57 x Hi67	Ki9 x Tzi18	45.7	30.2	44.3	48.2	42.10	
Hi57 x Hi26	Ki9 x Hi26	51.7	32.3	49.6	48.2	45.46	
Hi60 x Hi61	Mo17 x N3y	38.6	11.0	42.4	42.3	33.60	
Hi60 x Hi62	Mo17 x Pi17	42.9	21.2	41.7	27.4	33.29	
Hi60 x Hi65	Mo17 x Tx601	40.3	12.6	37.8	42.6	33.32	
Hi60 x Hi67	Mo17 x Tzi18	48.1	20.0	36.3	46.5	37.72	
Hi60 x Hi26	Mo17 x Hi26	36.1	13.5	48.4	44.5	35.62	
Hi61 x Hi62	N3y x Pi17	45.2	22.4	47.1	44.2	39.71	
Hi61 x Hi65	N3y x Tx601	43.4	12.4	46.0	50.1	37.97	
Hi61 x Hi67	N3y x Tzi18	39.4	22.5	44.9	46.8	38.38	
Hi61 x Hi26	N3y x Hi26	39.7	14.9	41.9	43.7	35.03	
Hi62 x Hi65	Pi17 x Tx601	50.2	26.2	50.8	45.4	43.14	
Hi62 x Hi67	Pi17 x Tzi18	36.6	23.8	39.1	37.4	34.21	
Hi62 x Hi26	Pi17 x Hi26	45.1	21.9	43.9	47.0	39.47	
Hi65 x Hi67	Tx601 x Tzi18	51.0	23.4	40.7	48.0	40.78	
Hi65 x Hi26	Tx601 x Hi26	45.0	19.0	51.1	52.9	42.00	
Hi67 x Hi26	Tzi18 x Hi26	44.7	28.1	44.2	50.2	41.79	
Hybrid mean		44.7	23.6	45.1	45.5	39.70	
$LSD_{0.05}$ Hybrids		10.5	7.8	8.4	13.3	10.23	
Grand Mean		40.3	20.5	40.0	40.1	35.21	
CV		11.4%	15.1%	8.8%	13.7%	12.06%	

7.2.1.6 Kernel density

Kernel densities among inbreds and hybrids varied among the four Waimanalo planting months with lesser coefficients of variability (Table 7.11). Mean kernel densities among inbreds were lowest in 8/04 and highest in the summer trials. Inbred kernel densities ranged from 1.111 g cm^{-3} (Hi60) to 1.218 g cm^{-3} (Hi53). Inbred Hi53 derived from a Cuban flint line was characterized by hard flint kernels. Analysis of variance (Sec 7.2.2) revealed no significant differences among inbreds and hybrids for kernel densities. Hybrid Hi62 x Hi65 had the highest kernel density (1.264 g cm^{-3}) (Table 7.11).

Table 7.11. Mean kernel density (g cm^{-3})across planting dates.

Cross	Pedigree	7/04	8/04	3/05	5/05	KDEN	Array
Inbreds	Pedigree						
Hi53	ICAL 210	1.181	1.091	1.419	1.181	1.218	1.19
Hi57	Ki9	1.183	1.127	1.097	1.278	1.172	1.20
Hi60	Mo17	1.193	1.013	1.087	1.149	1.111	1.18
Hi61	N3y	1.297	1.213	1.134	1.204	1.212	1.19
Hi62	Pi17	1.218	1.123	1.126	1.270	1.184	1.21
Hi65	Tx601	1.245	1.054	1.154	1.250	1.176	1.22
Hi67	Tzi18	1.265	1.147	0.929	1.239	1.145	1.21
Hi26	Hi26	1.189	0.978	1.073	1.228	1.117	1.19
Inbred mean		1.222	1.093	1.127	1.225	1.167	
$LSD_{0.05}$ Inbreds		0.07	0.32	0.46	0.30	0.32	
Hi53 x Hi57	ICAL 210 x Ki9	1.242	1.132	1.109	1.315	1.199	
Hi53 x Hi60	ICAL210 x Mo17	1.220	1.024	1.128	1.308	1.170	
Hi53 x Hi61	ICAL210 x N3y	1.219	1.069	1.100	1.250	1.160	
Hi53 x Hi62	ICAL210 x Pi17	1.225	1.128	1.113	1.248	1.179	
Hi53 x Hi65	ICAL210 x Tx601	1.277	1.147	1.145	1.309	1.219	
Hi53 x Hi67	ICAL210 x Tzi18	1.253	1.143	1.137	1.337	1.218	
Hi53 x Hi26	ICAL210 x Hi26	1.220	1.118	1.119	1.275	1.183	
Hi57 x Hi60	Ki9 x Mo17	1.208	1.166	1.093	1.259	1.181	
Hi57 x Hi61	Ki9 x N3y	1.271	1.146	1.177	1.315	1.227	
Hi57 x Hi62	Ki9 x Pi17	1.204	1.147	1.134	1.276	1.190	
Hi57 x Hi65	Ki9 x Tx601	1.266	1.114	1.161	1.304	1.211	
Hi57 x Hi67	Ki9 x Tzi18	1.170	1.175	1.144	1.306	1.199	
Hi57 x Hi26	Ki9 x Hi26	1.244	1.149	1.134	1.271	1.199	
Hi60 x Hi61	Mo17 x N3y	1.218	1.034	1.121	1.354	1.182	
Hi60 x Hi62	Mo17 x Pi17	1.280	1.140	1.135	1.265	1.205	
Hi60 x Hi65	Mo17 x Tx601	1.278	1.014	1.137	1.393	1.205	
Hi60 x Hi67	Mo17 x Tzi18	1.261	1.115	1.113	1.437	1.232	
Hi60 x Hi26	Mo17 x Hi26	1.205	0.892	1.092	1.275	1.116	
Hi61 x Hi62	N3y x Pi17	1.210	1.118	1.148	1.278	1.188	
Hi61 x Hi65	N3y x Tx601	1.262	1.114	1.148	1.264	1.197	
Hi61 x Hi67	N3y x Tzi18	1.256	1.149	1.142	1.262	1.202	
Hi61 x Hi26	N3y x Hi26	1.230	1.094	1.138	1.296	1.190	
Hi62 x Hi65	Pi17 x Tx601	1.287	1.150	1.130	1.487	1.264	
Hi62 x Hi67	Pi17 x Tzi18	1.256	1.136	1.143	1.279	1.204	
Hi62 x Hi26	Pi17 x Hi26	1.267	1.135	1.136	1.360	1.224	
Hi65 x Hi67	Tx601 x Tzi18	1.271	1.145	1.149	1.339	1.226	
Hi65 x Hi26	Tx601 x Hi26	1.275	1.063	1.137	1.451	1.232	
Hi67 x Hi26	Tzi18 x Hi26	1.250	1.125	1.156	1.272	1.201	
Hybrid mean		1.244	1.110	1.133	1.314	1.200	
$LSD_{0.05}$ Hybrids		0.10	0.08	0.04	0.24	0.14	
Grand mean		1.239	1.106	1.132	1.294	1.193	
CV		3.2%	6.7%	8.1%	8.9%	7.04%	

7.2.2. Analysis of variance for agronomic traits

7.2.2.1 Days to mid-anthesis and days to mid-silk

Analysis of variance was performed using the combined data from the four Waimanalo planting months for days to mid-anthesis and days to silk (Table 7.12). Months were significant for days to mid-anthesis ($P<0.01$). Replication within months was not significant. Inbreds, hybrids and the inbreds versus hybrids were significant ($P<0.01$). Entry x month interactions were significant for both inbreds and hybrids ($P< 0.01$) attributed largely to the autumn trial planted in 8/04 which was characterized by inadequate PAR and low temperature.

Days to mid-silk was also significant for months and were inconsistent across replications (Table 7.12). Inbreds, hybrids and inbreds versus hybrids were significant for days to mid-silk ($P<0.01$). Greater mean squares were observed for the inbreds versus hybrid suggesting the large difference of days to mid-silk between inbreds and hybrids among the four Waimanalo months as presented earlier (Table 7.2). Days to mid-silk were inconsistent across the four months for inbreds and hybrids ($P<0.01$).

7.2.2.2 Ear height and plant height

Months were significant for ear heights ($P<0.01$) (Table 7.12). Ear heights were inconsistent across replications ($P<0.01$). Inbreds and hybrids were significantly different for ear height ($P<0.01$). The mean squares of hybrids were higher than the inbreds indicating more variability. The inbreds versus hybrids was also significant

Table 7.12. Mean squares from the ANOVA for traits across Waimanalo seasons.

Source		DTA	DTS	EH	PH	ED	EL
Months	3	2,050.26 **	2,218.31 **	12,060.88 **	15,933.9 **	5.577 **	373.35 **
Reps in Months	4	2.60 ns	3.54 *	256.27 **	449.7 **	0.022 ns	0.48 ns
Entries	35	47.10 **	65.23 **	3,078.44 **	6,806.8 **	1.449 **	32.27 **
Inbreds	7	43.07 **	74.46 **	466.31 *	1,214.1 **	1.043 **	16.87 **
Hybrids	27	13.19 **	18.83 **	911.41 **	1,250.7 **	0.695 **	12.16 **
I vs H	1	991.07 **	1,253.35 **	79,873.05 **	195,971.0 **	24.628 **	683.04 **
Entry x Month	105	2.42 **	3.09 **	102.47 **	162.8 **	0.069 **	1.73 **
Inbreds x M	21	2.18 **	3.93 **	179.01 **	278.4 **	0.146 **	2.42 **
Hybrids x M	81	1.90 **	2.31 **	75.40 **	133.8 **	0.047 **	1.58 *
(I vs H) x M	3	18.04 **	18.34 **	297.71 **	137.3 ns	0.129 **	0.79 ns
Pooled Error	140	1.09	1.43	44.71	76.1	0.027	1.09
Total	287						
Mean		55.6	57.0	114.2	215.5	4.5	17.7
CV %		1.88%	2.10%	5.85%	4.05%	3.66%	5.91%
$LSD_{0.05}$ Inbreds		1.99	2.48	14.57	19.72	0.42	2.52
$LSD_{0.05}$ Hybrids		2.40	2.63	15.35	19.89	0.35	2.33

Source		KN	KRN	KW	YLD	KDEN
Months	3	1,350.24 **	6.53 **	56,788.59 **	6,907.20 **	0.565 **
Reps in Months	4	10.30 ns	0.19 ns	401.86 **	28.39 ns	0.004 ns
Entries	35	238.81 **	17.63 **	4,167.51 **	700.98 **	0.009 ns
Inbreds	7	79.74 **	28.39 **	2,414.12 **	118.14 **	0.013 ns
Hybrids	27	55.83 **	14.11 **	2,204.71 **	124.21 **	0.006 *
I vs H	1	6,292.63 **	37.38 **	69,436.95 **	20,353.89 **	0.055 ns
Entry x Month	105	8.19 *	0.69 *	529.90 **	43.20 **	0.006 ns
Inbreds x M	21	8.68 ns	1.79 **	706.02 **	29.35 *	0.015 **
Hybrids x M	81	8.25 *	0.32 ns	471.03 **	37.95 **	0.004 ns
(I vs H) x M	3	3.21 ns	3.11 **	886.69 **	282.01 **	0.018 ns
Pooled Error	140	5.58	0.46	89.13	18.03	0.007
Total	287					
Mean		34.5	13.4	158.2	35.2	1.2
CV %		6.84%	5.08%	5.97%	12.06%	7.04%
$LSD_{0.05}$ Inbreds		5.07	1.49	20.09	6.45	0.32
$LSD_{0.05}$ Hybrids		5.32	1.50	21.21	10.23	0.14

(P<0.01). Ear heights among inbreds and hybrids were inconsistent across months (P<0.01).

Plant heights varied greatly also for months (P<0.01) (Table 7.12) as it was for ear heights. Replications within months were significant (P<0.01), indicating that plant heights were inconsistent across replications. Variation among inbreds were significant (P<0.05). The hybrids obtained greater variations in plant height (P<0.01). Inbreds versus hybrids were also significant. The interaction among inbreds and hybrids with the months were highly significant (P<0.01), indicating that plant heights were inconsistent across months. The variations among inbreds versus hybrids were consistent across months. The seasonal differences were attributed mainly to the autumn trial in 8/04.

7.2.2.3 Ear diameter and ear length

Months were significant for ear diameters (P<0.01) and were consistent across replications (Table 7.12). Variation among inbreds and hybrids varied greatly for ear diameter (P<0.01). Inbreds versus hybrids for ear diameter were significant as it was for most traits (P<0.01). Ear diameters were inconsistent among the four months (P<0.01) for both inbreds and hybrids.

Ear lengths were also significant for months (P<0.01) and consistent across replications (Table 7.12). Both inbreds and hybrids varied greatly for ear length (P<0.01). As for most traits, the inbreds versus hybrids were also highly significant for ear length (P<0.01). The inbreds and hybrid interactions with the months were significant indicating that ear lengths were inconsistent across months.

7.2.2.4 Kernel numbers and kernel row numbers

Month variations were significant for kernel numbers and were consistent across replications (Table 7.12). Variation among inbreds were significant and larger than the hybrids for kernel numbers ($P<0.01$). Differences between inbreds and hybrids for kernel numbers were also significant ($P<0.01$). Variations for kernel numbers among inbreds were not significant across months. The hybrids interacted significantly with the months ($P<0.05$). The variations between inbreds and hybrids for kernel number were consistent across months.

Kernel row numbers varied greatly for months ($P<0.01$) and were consistent across replications as it was for kernel numbers (Table 7.12). Variations among inbreds and hybrids were significant ($P<0.01$). Comparisons between inbreds and hybrids were also significant for kernel row numbers ($P<0.01$). Kernel row numbers were inconsistent for inbreds ($P<0.01$) across months. Hybrids did not interact significantly with months.

7.2.2.5 Kernel weight and plant yield

Variations for months for kernel weight were very large ($P<0.01$) (Table 7.12). Replications within months were significant ($P<0.01$) indicating that kernel weights were variable between replications. Variations in kernel weights among inbreds ($P<0.01$) were greater than variations among the hybrids ($P<0.01$). Kernel weights varied greatly between inbreds and hybrids ($P<0.01$). Kernel weights among inbreds and hybrids interacted significantly with the months ($P<0.01$). The significant genotypes by month

interactions for kernel weight are attributed mainly to the autumn trial planted in 8/04 that had inadequate PAR and low temperature during the grain filling duration.

Month variances were also very large for plant yields as it was for kernel weights ($P<0.01$) (Table 7.12). Replication variances within months were not significant for plant yields. Variations for plant yields were significant among inbreds, hybrids, inbreds versus hybrids ($P<0.01$) and interacted significantly with months ($P<0.01$) (Table 7.12).

7.2.2.6 Kernel density

Seasonal variations for kernel density were significant ($P<0.01$) (Table 7.12). Unlike most agronomic traits studied, variations among inbreds for kernel density were not significant. Significant differences were found among hybrids. Variations of kernel densities between inbreds and hybrids were not significant ($P<0.05$). Kernel densities were inconsistent for inbreds across months ($P<0.01$). Hybrid kernel densities were consistent across months as shown by hybrids x month interaction that was not significant.

7.2.3 Estimation of general and specific combining ability effects

7.2.3.1 Days to mid-anthesis and mid-silking

Inbred Hi60 bred to mature early greatly reduced days to mid-anthesis as shown by its low GCA (Table 7.13). Inbred Hi26 increased days to mid-anthesis as shown by its high GCA (Table 7.13). Other inbreds that reduced days to mid-anthesis include Hi67 (-0.89), Hi53 (-0.53), Hi61 (-0.17), and Hi57 (-0.07). For SCA analysis, SCA effects ranged from -2.19 (Hi57 x Hi26) to 1.00 (Hi53 x Hi61) (Table 7.13). Negative SCA effects were observed in all hybrids with Hi65 and Hi67, while positive SCA effects were observed in Hi57 x Hi26 (0.47) and Hi57 x Hi62 (0.06).

Days to mid-silking was reduced by Hi60 having the most negative GCA, a temperate inbred as mentioned previously, selected for earliness (Table 7.14). Other inbreds that greatly reduced days to mid-silk were Hi67 (-1.07), Hi53 (-0.83) and Hi57 (-0.68). Inbred Hi26 having the highest GCA greatly increased days to mid-silking as it did for days to mid-anthesis. Among the hybrids, negative SCA effects were in all crosses between Hi62, Hi65 and Hi67 as either parents. Specific combing ability effects for DTS ranged from -2.13 (Hi53 x Hi65) to 2.29 (Hi53 x Hi61) followed by Hi57 x Hi67 (0.22). These were only the two hybrids that gave positive SCA effects for DTS.

Table 7.13. GCA (below diagonal) and SCA effects for DTA across Waimanalo planting dates.

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**-0.53**	-1.73	-1.19	1.00	-1.48	-1.58	-1.03	-1.23
Hi57		**-0.07**	-0.40	-1.21	0.06	-1.04	-0.11	-2.19
Hi60			**-1.48**	-1.18	-1.15	-1.50	-0.83	0.47
Hi61				**-0.17**	-1.34	-0.69	-1.39	-1.96
Hi62					**0.68**	-1.16	-1.36	-0.94
Hi65						**1.16**	-0.59	-1.16
Hi67							**-0.89**	-0.86
Hi26								**1.31**

Table 7.14. GCA (below diagonal) and SCA effects for DTS across Waimanalo environments

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**-0.83**	-1.27	-1.31	2.29	-1.91	-2.13	-0.38	-1.03
Hi57		**-0.68**	-0.33	-1.98	-0.31	-0.53	0.22	-1.93
Hi60			**-1.39**	-1.52	-1.47	-2.07	-1.32	-0.22
Hi61				**-0.12**	-1.62	-1.35	-1.47	-1.75
Hi62					**0.96**	-1.17	-1.92	-1.70
Hi65						**1.43**	-0.77	-1.42
Hi67							**-1.07**	-0.80
Hi26								**1.71**

7.2.3.2 Ear height and plant height

General and specific combining ability effects were determined for plant height and ear heights across months. Selection for short ear heights and plant heights has been a routine activity in maize breeding. Inbreds Hi60, Hi67 and Hi61 greatly reduced ear heights as shown by their highly negative GCA effects (Table 7.15). Ear heights were greatly increased by tropical inbreds Hi65, Hi57, Hi26, and Hi62 as shown by positive GCA effects (Table 7.15). Among hybrids, the lowest SCA effects were in Hi61 x Hi67 (-1.58) and Hi53 x Hi60 (-0.58). Hybrids with higher SCA effects for ear heights were Hi53 x Hi61 (31.52), Hi57 x Hi65 (14.93), Hi62 x Hi26 (14.19) and Hi65 x Hi26 (12.69).

Plant heights were greatly reduced by inbreds Hi67, Hi60, Hi57, Hi53 and Hi62 as shown by negative GCA effects (Table 7.16) while plant heights were increased by Hi65, Hi61and Hi26 as shown by positive magnitudes of GCA effects (Table 7.16). For the SCA analysis, magnitudes for SCA effects were observed to be positive for all the 28 hybrids. Specific combining ability effects for PH was lowest for Hi60 x Hi62 (3.31) and highest for Hi53 x Hi61 (25.46). Higher SCA hybrids following Hi53 x Hi61 were, Hi57 x Hi65 (21.98), Hi62 x Hi26 (20.66) and Hi65 x Hi26 (19.12).

Table 7.15. GCA (below diagonal) and SCA effects for EH across Waimanalo planting dates.

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**1.37**	9.22	-0.58	31.52	6.49	11.12	9.37	7.04
Hi57		**3.63**	0.66	8.76	10.36	14.93	10.30	5.22
Hi60			**-10.95**	7.40	2.56	5.50	12.19	11.80
Hi61				**-0.98**	8.66	8.16	-1.58	4.34
Hi62					**2.73**	11.14	10.45	14.19
Hi65						**6.73**	10.71	12.69
Hi67							**-5.46**	**6.63**
Hi26								**2.93**

Table 7.16. GCA (below diagonal) and SCA effects for PH across Waimanalo planting dates.

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**-1.99**	10.88	6.36	25.46	9.84	17.11	17.93	16.52
Hi57		**-4.92**	9.29	12.14	14.40	21.98	16.48	10.95
Hi60			**-7.40**	11.99	3.31	14.02	14.71	18.93
Hi61				**10.25**	16.42	16.00	8.38	8.41
Hi62					**-0.88**	14.44	10.23	20.66
Hi65						**11.53**	14.72	19.12
Hi67							**-10.16**	9.75
Hi26								**3.57**

7.2.3.3 Ear diameter and ear length

Combining ability effects for ear diameter using the combined data are presented on Table 7.17. Inbreds Hi57, Hi65 and Hi53 increased ear diameters as shown by positive GCA effects. Ear diameters were slightly reduced by inbreds Hi60, Hi61 and Hi26 as shown by their negative GCA effects. For SCA combinations, highest SCA effects for ED were in Hi53 x Hi61 (0.39) followed by Hi57 x Hi65 (0.31). Lowest SCA effects were in Hi60 x Hi65 (-0.12) and Hi57 x Hi60 (-0.07).

Inbred Hi60 greatly increased ear lengths by having the most positive GCA effect. These were followed by inbreds Hi61 and Hi53 (Table 7.18). Ear lengths were reduced by Hi62, Hi65 and Hi57 as shown by their negative GCA effects. Among the hybrids, SCA effects ranged from -0.49 (Hi62 x Hi67) to 1.96 (Hi60 x Hi67). Hybrids with high SCA effects included, Hi53 x Hi26 (1.78), Hi57 x Hi65 (1.47), Hi62 x Hi65 (1.38) and Hi61 x Hi62 (1.31).

7.2.3.4 Kernel numbers and kernel row numbers

Inbreds Hi60, Hi65 and Hi67 increased kernel numbers, while inbreds Hi53, Hi57, Hi61, Hi26 and Hi62 (-0.29) reduced kernel numbers (Table 7.19). Negative SCA effects for kernel numbers were observed in three hybrids (Table 7.19). These were Hi62 x Hi67 (-0.59), Hi53 x Hi57 (-0.46) and Hi61 x Hi65 (-0.30). Higher SCA effects were in Hi62 x Hi26 (6.21), Hi65 x Hi26 (6.00), Hi53 x Hi61 (5.01) and Hi57 x Hi65 (4.26).

The magnitudes of GCA and SCA effects were determined for kernel row numbers across the four Waimanalo months (Table 7.20). Inbreds with positive GCA

Table 7.17. GCA (below diagonal) and SCA effects for ED across Waimanalo planting dates.

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**0.12**	0.13	0.08	0.39	0.19	0.15	0.02	0.17
Hi57		**0.22**	-0.07	0.20	0.06	0.31	0.26	0.15
Hi60			**-0.33**	*0.12*	0.14	-0.12	0.07	0.28
Hi61				**-0.23**	0.13	0.19	0.11	0.13
Hi62					**0.13**	0.29	0.15	0.12
Hi65						**0.17**	0.28	0.24
Hi67							**0.02**	0.20
Hi26								**-0.10**

Table 7.18. (below diagonal) and SCA effects for EL across Waimanalo planting dates.

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**0.35**	-0.04	1.21	1.27	0.36	1.35	0.91	1.78
Hi57		**-0.13**	1.10	0.33	0.15	1.47	0.03	1.29
Hi60			**1.19**	0.58	0.91	0.23	1.96	0.42
Hi61				**0.42**	1.31	0.19	1.14	0.54
Hi62					**-1.20**	1.38	-0.49	1.28
Hi65						**-1.01**	-0.13	1.30
Hi67							**0.18**	1.19
Hi26								**0.20**

Table 7.19. GCA (below diagonal) and SCA effects for KN across Waimanalo planting dates.

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**-1.43**	-0.46	3.89	5.01	0.31	2.32	0.68	2.65
Hi57		**-0.72**	2.42	0.80	1.07	4.26	0.32	3.92
Hi60			**2.31**	3.01	2.24	3.94	3.07	4.23
Hi61				**-0.56**	3.01	-0.30	1.57	2.29
Hi62					**-0.29**	2.15	-0.59	6.21
Hi65						**1.03**	1.72	6.00
Hi67							**0.14**	4.23
Hi26								**-0.48**

Table 7.20. GCA (below diagonal) and SCA effects for KRN across Waimanalo planting dates.

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**0.23**	-0.07	0.40	0.88	0.30	0.01	-0.12	0.58
Hi57		**1.02**	0.12	0.22	0.36	0.72	0.64	-0.38
Hi60			**-1.30**	-0.27	0.13	-0.35	0.36	0.41
Hi61				**-1.48**	0.16	0.29	0.04	0.11
Hi62					**-0.15**	0.11	0.10	-0.52
Hi65						**0.90**	0.16	0.59
Hi67							**1.03**	0.41
Hi26								**-0.25**

effects increased kernel row numbers. These were Hi67 (1.03), Hi57 (1.02), Hi65 (0.90) and Hi53 (0.23). Inbred Hi61 reduced kernel row numbers as indicated by the negative GCA effect (-1.48). Specific combining ability effects ranged from -0.52 (Hi62 x Hi26) to 0.88 (Hi53 x Hi61). Hybrids with high SCA effects following Hi53 x Hi61 include Hi57 x Hi65 (0.72) and Hi57 x Hi67 (0.64).

7.2.3.5 Kernel weight and plant yield

Kernel weights were increased by Hi53, Hi57, Hi61 and Hi62 as shown by their positive GCA effects (Table 7.21). These inbreds were characterized as having large kernels and hence gave higher GCA effects for kernel weights. Kernel weights were reduced by inbreds Hi60, Hi65 and Hi67 (Table 7.21) that had smaller kernel sizes and thus reduced GCA effects for kernel weight. The reduction in kernel weights by inbred Hi60 is actually compensated by its ability to increase kernel numbers (Table 7.20). For SCA analysis, SCA effects among the hybrids for kernel weight ranged from -10.97 (Hi60 x Hi65) to 20.25 (Hi61 x Hi62). Only two out of the 28 hybrids had negative SCA effects for kernel weight; Hi57 x Hi62 (-1.42) and Hi60 x Hi65 (-10.97).

Plant yields were increased by inbreds Hi53, Hi57 and Hi65 as shown by their positive GCA effects (Table 7.22). Inbreds Hi60, Hi61, Hi62 and Hi26 were characterized by much smaller ears size, and reduced plant yields. Among hybrids, SCA effects ranged from -0.28 (Hi60 x Hi65) to 9.82 (Hi57 x Hi65). Inbred Hi65 was the parent in both hybrids that had the opposing SCA effects. Most hybrids had positive SCA effects for plant yield except for Hi60 x Hi65 (-0.28) and Hi62 x Hi67 (-0.11).

Table 7.21. GCA (below diagonal) and SCA effects for KW across Waimanalo planting dates.

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**10.17**	3.74	1.30	8.29	11.95	15.63	10.45	9.52
Hi57		**4.22**	1.54	14.27	-1.42	4.85	3.95	17.04
Hi60			**-7.02**	18.98	19.62	-10.97	10.67	2.85
Hi61				**16.81**	20.25	8.10	5.79	3.63
Hi62					**2.41**	18.88	0.69	7.58
Hi65						**-12.14**	8.26	0.48
Hi67							**-12.47**	16.46
Hi26								**-1.99**

Table 7.22. GCA (below diagonal) and SCA effects for YLD across Waimanalo planting dates.

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**1.30**	1.30	4.02	7.89	5.38	5.05	3.02	6.66
Hi57		**3.30**	2.08	6.00	1.88	9.82	3.64	8.15
Hi60			**-3.07**	2.37	1.98	-0.28	5.63	4.68
Hi61				**-0.91**	6.25	2.21	4.14	1.93
Hi62					**-0.83**	7.30	-0.11	6.29
Hi65						**1.47**	4.15	6.52
Hi67							**-0.05**	7.83
Hi26								**-1.20**

7.2.3.6 Kernel density

General and specific combining ability effects for kernel density are presented on Table 7.23. Inbreds Hi61, Hi62, Hi65and Hi67 increased kernel densities while inbreds Hi60 and Hi26 greatly reduced kernel densities. For SCA analysis, SCA effects ranged from -3.95 (Hi53 x Hi61) to 5.76 (Hi60 x Hi67). Higher SCA effects for kernel density were in Hi62 x Hi65 (4.50), Hi62 x Hi26 (3.85) and Hi65 x Hi26 (3.72). Several hybrids had negative SCA effects for kernel density.

7.2.4 Analysis of variance for general and specific combining ability effects

Analysis of variance for combining ability effects showed that both GCA and SCA were important in the genetic control of days to mid-anthesis and days to mid-silk (Table 7.24). Highly significant differences for GCA ($P<0.01$) and SCA effects ($P<0.01$) were observed for both traits. The ratio of GCA to SCA mean squares was 1.98 for days to mid-anthesis, and 2.20 for days to mid-silk suggesting that additive gene effects were more prevalent in the genetic control of both traits. Both GCA and SCA month interactions were significant ($P<0.01$) suggesting that GCA and SCA effects were inconsistent for days to mid-anthesis and days to mid-silk across the four Waimanalo planting months.

Variation for both GCA and SCA effects were significant for plant height and ear height ($P<0.01$) (Table 7.24). Non-additive gene effects were prevalent for ear height and plant heights. Ratios of GCA to SCA mean squares were 0.58 and 0.49 for ear height and plant height, respectively, suggesting the predominance of non-additive gene effects.

Table 7.23. GCA (below diagonal) and SCA effects for KDEN (x100) across Waimanalo planting dates.

	Hi53	Hi57	Hi60	Hi61	Hi62	Hi65	Hi67	Hi26
Hi53	**0.30**	0.21	-0.34	-3.95	-2.58	0.66	1.83	0.28
Hi57		**0.16**	0.91	2.92	-1.30	-0.02	0.08	2.07
Hi60			**-2.22**	0.75	2.57	1.78	5.76	-3.90
Hi61				**0.36**	-1.67	-1.66	0.24	0.89
Hi62					**0.88**	4.50	-0.14	3.85
Hi65						**1.71**	1.23	3.72
Hi67							**0.37**	2.01
Hi26								**-1.55**

Table 7.24. Mean squares from the analysis of variance for combining ability across Waimanalo months.

Source	df	DTA	DTS	EH	PH	ED	EL
GCA	7	38.95 **	57.88 **	1296.98 **	2500.22 **	1.61 **	24.30 **
SCA	20	27.58 **	36.82 **	2239.69 **	5080.91 **	0.71 **	19.73 **
GCA x M	21	1.25 **	1.91 **	98.02 **	179.18 **	0.10 **	2.04 **
SCA x M	84	1.20 **	1.46 **	39.54 **	56.95 *	0.02 *	0.57 ns
Pooled error		0.74	0.76	0.54	38.07	0.82	0.71
Ratio							
GCA:SCA		1.41	1.57	0.58	0.49	2.28	1.23
2GCA/(2GCA+SCA)		0.74	0.76	0.54	0.50	0.82	0.71

Source	df	KN	KRN	KW	YLD	KDEN
GCA	7	55.00 **	39.46 **	4376.13 **	154.86 **	0.0065 ns
SCA	20	189.71 **	1.62 **	2114.93 **	559.16 **	0.0054 **
GCA x M	21	7.08 ns	0.56 **	1037.12 **	40.85 **	0.0058 ns
SCA x M	84	3.35 ns	0.29 ns	71.91 **	16.79 **	0.0025 ns
Pooled error		2.79	0.23	0.805	0.356	2.79
Ratio						
GCA:SCA		0.29	24.37	2.07	0.28	1.21
2GCA/(2GCA+SCA)		0.37	0.98	0.81	0.36	0.71

General combining ability and specific combining ability x month interactions were significant for ear height and plant height (Table 7.24).

Ear diameters and ear lengths were significant for GCA and SCA effects (Table 7.25). Ratio of GCA to SCA mean squares was 2.28 for ear diameter and 1.23 for ear length which suggest that both traits are controlled by the additive type of gene action. General combining ability effects were not consistent across months for ear length and ear diameter. Ear diameters were significant for SCA x month interactions. Specific combining abilities were consistent across months for ear length.

General and specific combining ability effects were also significant ($P<0.01$) for kernel numbers (Table 7.24). Mean squares of SCA were three times larger than GCA suggesting that non-additive gene effects were prevalent in the genetic control of kernel numbers (Ratio of GCA: SCA = 0.29). General combining ability and specific combining ability x month interactions were not significant for kernel numbers.

Both GCA and SCA effects were significant for kernel row numbers. Additive gene effects were prevalent for kernel row numbers as shown by a high ratio of GCA to SCA (24.4) (Table 7.24). General combining ability x month interactions were significant. Specific combining ability effects for kernel row numbers were consistent across months.

Kernel weight and plant yield were also significant for GCA and SCA effects ($P<0.01$) (Table 7.24). Kernel weights were predominantly controlled by additive gene effects (GCA:SCA= 2.1). The ratio of GCA to SCA for single ear weights was 0.28

suggesting the predominance of non-additive gene effects. Both GCA and SCA x month interactions were significant for kernel weight and plant yield.

Variations for GCA were not significant for kernel density (Table 7.24). Specific combining abilities were significant ($P<0.01$). General and specific combining ability x month interactions were not significant, suggesting that GCA and SCA effects were consistent across months.

7.3 Discussions

7.3.1 Mean performance and analysis of variance

Means of the agronomic traits varied extensively among the four planting dates. The differences in performances of inbreds and hybrids among planting dates are attributed mainly to the effects of climatic conditions as described previously (Chapter 5). Mean performances of traits were generally low in the autumn planting in August because of low PAR and temperature that declines through September to November in Waimanalo (Figure 2.1 and 2.2, Chapter 2). Higher means for most agronomic traits occurred in the May and July plantings in which the first two months of growth are under high PAR and temperature. Light as emphasized by Jong et al. (1982) in Waimanalo is highly correlated with maize grain and its components.

Coefficients of variation were low among the planting dates for most agronomic traits reflecting well managed plots and homogeneity of Waimanalo soils that had been planted exclusively to corn since 1961 (Brewbaker, 1985). Days to mid-anthesis and days to mid-silk were longer in the 3/05 planting. This was attributed to the low temperatures during the first 30 days of growth (23.8°C, Figure 2.1) which delayed anthesis and silking. Ear heights and plant heights were tallest in 7/04 and 5/05 summer trials attributed to high PAR. Low PAR in the 8/04 trial resulted to shorter ear diameters and ear lengths. Mean kernel numbers among entries were higher for the summer planting. Mean kernel row numbers were consistent among the four planting dates. Kernel weights and plant yields were two times higher in the summer plantings in 7/04, 3/05 and 5/05 relative to the autumn planting in 8/04 which received the least amounts of

PAR during the growth period. Mean kernel densities were consistent among the four Waimanalo planting dates.

Months were highly significant for most agronomic traits. Variations among replications were not significant for most traits reflecting the homogenous experimental plots at Waimanalo. Most agronomic traits among inbreds and hybrids varied significantly across months. Entries x month interactions were highly significant among inbreds and hybrids for most agronomic traits. The significant genotype by month interactions were attributed mainly to the autumn trial planted in 8/04 that received the lowest amount of light.

7.3.2 Diallel analysis of agronomic traits

Inbred Hi60 derived from Mo17 reduced days to mid-anthesis and days to mid-silking as shown by negative GCA effects. This was expected of Hi60 since it was selected for early maturity to avoid frost damage in short growing months in the temperate region of the US. Inbred Hi60 also reduced ear heights and plant heights and increased kernel numbers. Tropical inbreds Hi57 and Hi67 increased kernel row numbers. Kernel weight and plant yields were reduced by the Hi60 parent. This was expected because this inbred had smaller kernels and smaller ears. Inbred Hi61 having large kernels greatly increased kernel weights. The reduction in kernel and plant yield by Hi60 however was compensated its ability to greatly increase kernel numbers and ear lengths. Kernel densities were also reduced by Hi60 and increased by tropical flint inbred Hi65.

General and specific combining ability effects were both significant for days to mid-anthesis and days to mid-silking. Ratios of GCA to SCA mean squares revealed that both days to mid-anthesis and days to mid-silk were controlled primarily by additive gene effects. Previous studies have shown the predominance of additive gene effects for days to silking. Significant GCA and SCA effects for days from planting to silking were reported by Katsantonis et al. (1986). The GCA mean squares were larger than SCA mean squares indicating that additive gene effects are most predominant for days to silking. Similarly, Wang et al. (1999), and Cross (1975) also reported larger GCA mean squares than SCA for days to silking. The prevalence of additive gene effects for days to anthesis and silking under Waimanalo planting months were also reported by Logrono (1990).

Ear heights and plant heights were controlled by non-additive gene effects, while ear diameters and ear lengths were controlled primarily by additive gene effects. Non-additive gene effects were predominant in the control of kernel numbers and plant yields. These corroborates with the study of Wang et al. (1999) who also reported greater SCA mean squares for yield per plant and kernel numbers. Genetic control of kernel weight was controlled by additive gene effects. Wang et al. (1999) reported greater GCA mean squares (males and female effects) for kernel weight in maize.

General combining ability and specific combining ability x month interactions were highly significant for most traits except for kernel numbers and kernel density, indicating large monthal effects in the expression of additive and non-additive gene effects.

The importance of kernel density has been emphasized in a previous study (Thompson and Goodman, 2006) and therefore was included in this study. Dense kernels are preferred for alkaline cooking processes for making *masa*, tortilla chips and snack foods. There is also some limited evidence that dense kernels will increase ethanol yield (Murthy et al., 2004). Analysis of variance for combining ability effects showed the significance of SCA effects for kernel density. However the ratio of GCA to SCA effects (1.2) for this trait suggests that this trait is controlled primarily by additive gene effects. General combining ability x month interaction was not significant indicating that GCA effects for kernel density were consistent across months.

Breeding methods that take advantage of additive variation are required for improvement of traits with significant additive gene effects. Improvement of traits with significant non-additive gene effects would require hybrid breeding approaches. The significance of entry by month interactions for most agronomic traits requires selection and evaluation in multiple months or environments.

CHAPTER 8
CONCLUSIONS AND RECOMMENDATIONS

The amount of genetic variability of GFR and GFP among topical maize germplasm permits breeding for increased GFR and extending GFP to increase yield potential of tropical maize. Inbred performances for GFR and GFP were significantly correlated with the hybrid array means. Inbreds Hi53 and Hi61 consistently increased GFR among Waimanalo months. In the autumn trial, inbred Hi57 increased GFP while inbred Hi60 reduced GFP. Grain filling periods were reduced by Hi57 and increased by Hi60 in the summer trials.

Grain filling rate and grain filling period in tropical maize are controlled primarily by additive gene effects. Alteration of these traits would therefore require breeding methods that exploit additive variation such as those used in population improvement. Hybrid breeding methods could also be used considering the significant SCA effects for GFR and GFP. The highly significant entry x month interactions for GFR and GFP in Hawaii mandates breeding and evaluation in multiple planting dates through the year.

Generation mean analyses of GFR and GFP data revealed little evidence of departure from a simple model of additive and dominance variance, without compelling interactions. In some cases, the ad interactions were significant for GFR and the dd interactions significant for GFP. Hybrid vigor in GFR and GFP was evident in both the F1 and F2 populations, and in backcross populations, and the significance of dominance effects. Genetic effects were mostly confounded with the interaction components and seasons. Selections of inbreds with consistent performance for GFR and GFP under

specific planting dates are recommended for a future study. The confounding effects of heterosis could be reduced by the use of recombinant inbred lines (RILs) which allow the evaluation of fixed inbred genotypes across different planting dates and identify putative QTLs associated with GFR and GFP.

The high correlations between kernel weights and grain filling rates indicate that kernel weights may be used as an effective selection index for grain filling rates in tropical maize germplasm. Inbred Hi61 characterized by large kernels had the highest mean GFR and highest mean kernel weight. Multiple regression analysis showed that light measured as photosynthetic active radiation during the effective filling period duration in Waimanalo accounted for most of the variation in GFR, GFP, kernel weight, plant yield and kernel numbers as opposed to temperature.

Chlorophyll concentration was increased by inbred Hi60, a temperate dent from Mo17, in all three growth stages consistent in the summer trials under high PAR and temperature. Inbred Hi26 also consistently increased chlorophyll at 60 and 90 DAP. Inbreds Hi65 and Hi61 reduced chlorophyll concentration in all growth stages.

Additive gene effects were prevalent for chlorophyll concentrations among the three growth stages, among seasons, and the combined analysis. With the consistency of these effects it may be possible to do selections for increased chlorophyll concentration in any of the three growth stages using a SPAD meter. However selection is best at 60 days after planting because of much lower error variances. The use of a SPAD meter allows rapid and non-destructive determination of chlorophyll concentration. Breeding therefore for increased chlorophyll concentration in tropical maize could be achieved using

methods that exploit additive variation. Selection for increased chlorophyll concentration per se however may not significantly improve maize grain yield. Chlorophyll concentrations in all the three growth stages were not significantly correlated with kernel weights and plant yield. Other traits, such as leaf area, leaf number and "stay green" (leaf area duration) should also be studied in relation to SPAD.

Additive gene effects were prevalent for days to mid-anthesis, days to mid-silk, ear diameter, ear length, kernel row numbers and kernel density. Ear height, plant height, kernel number and plant yield were controlled primarily by non-additive gene effects. The agronomic data provides additional information on the inbreds used in this study that were previously released for public use. Seeds of these inbreds are available upon request.

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